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THE CONSERVATION OF JUNIPER: LONGEVITY AND OLD AGE

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SUMMARY

(1) The life-span of juniper, *Juniperus communis communis* L. appears to be about 100 years in southern England on the chalk; whereas in the north of England exceptional individuals reach over 200 years.

(2) Longevity may be related to growth rate; slower growing junipers can live longer, and the life-span can be correlated with the growth rate in the early years. Variability of growth rates makes comparison of trunk girths of specimens from different sites very unreliable as a basis for estimating age.

(3) Seed production in older junipers is reduced. Sex ratios are often not 1:1, and past history may be a factor in explaining sex ratios of present-day populations.

(4) Juniper populations are often roughly even-aged, and in these cases study of the age and expected longevity of the bushes allows for prediction of the ultimate life-span of such populations in the absence of regeneration. This is relevant to the management of juniper on nature reserves.

INTRODUCTION

The longevity of plants of conservation interest is of obvious importance in the management of nature reserves. Where there is clonal growth a plant may be able to survive for very long periods, but in the absence of clonal growth, senescence and death are likely to occur at a time characteristic for the species. Reproduction by seed is important in all species for the colonization of new areas, but for non-clonally growing species it is vital that this be successful before the old plants die.

Juniper, *Juniperus communis* L., is a plant which grows clonally only under certain special conditions which are rare in lowland England. In these areas too, populations of juniper often have few age classes, reflecting periods in their past history when successful regeneration occurred (Ward 1981). This means that whole populations may become senescent and die at roughly the same time. Historical information also points to the decline and loss of juniper sites because of the life-span of the bushes (Ward 1973). Preliminary studies of the longevity of lowland juniper, *J. communis communis* L. have therefore been made to provide information on which to base the management of this plant on nature reserves. Other characteristics of old junipers including size, growth, reproductive success and sex ratio are also discussed briefly.

METHODS AND STUDY SITES

Juniper samples were collected for ring counts from various sites in England. It was not normally possible to take many specimens of old living junipers, although there was an opportunity to do so at Porton Down, Hampshire. Dead junipers however can be cut without serious destruction to sites of conservation interest. Dead specimens were collected

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casually at first, but later were taken from sites known to have many old, dead and dying bushes. Specimens which died in unshaded situations and which had no obvious injuries were sampled. It was hoped that this excluded some factors of mortality which are not related to intrinsic life-span.

Basal sections of the trunks were examined. While juniper is relatively resistant to rotting, older and dead junipers may have basal rot holes. These specimens were not included in the analysis if the gap in the ring count was estimated to be more than 10 years by comparison with the remaining rings. Growth measures used included the circumference of the trunk at the base (girth), and the length of the longest radius of the cut surface. Ring counts and measurements of ring widths were taken along this radius. This procedure is not entirely satisfactory, but limitations are imposed by the marked asymmetry of stem growth of many junipers. Cankering, rotting and the tendency of branches to fall from the upright position cause very irregular growth, sometimes entirely one-sided. Changes in grazing levels also affect growth. Asymmetric growth may begin at any age, but is usually more apparent after about 30 years. Generally the longest radius includes that part of the circumference which is still growing when all the rest is dead—a common occurrence in old junipers.

Populations were normally studied in May when the sexes are most easily distinguishable. Some bushes recorded as sterile may flower sparsely or infrequently. Counts of bushes were made on 10 m wide transects across the stands.

Sites for which new data are presented in this paper are listed here in county order together with their National Grid References: Buckinghamshire—Lodge Hill SU794002; Cumbria—Mollen Wood, nr Bewcastle NY561708, Oxenfell NY321019, Whitbarrow SD442893; Dumfries—Tynron Juniper Wood NNR NX82–92; Durham—Waskerley Beck NE063430; Gloucestershire—Juniper Hill, Edgeworth SO928058; Hampshire—Porton Down 'Breck' SU248381, Stockbridge Down SU382349; Northumberland—Kyloe Crags NU050388, The Bog NY686542; Oxfordshire—Beacon Hill, Aston Rowant NNR SU727973, Bix Bottom SU721878, Chinnor Hill SU765005; Surrey—Park Downs TQ267586; Sussex—Kingley Vale NNR SU817112; Wiltshire—Bulford Downs SU205441, Pepperbox Hill SU214248, Porton Roche Court (young bushes) SU243363, Porton Roche Court (old bushes) SU245363, Porton Blakes Firs SU237361; Yorkshire—Moughton Fell SD797704.

RESULTS

Life-span

The ages of junipers are shown by assembling all known records of ring counts of junipers of over 70 years for live or dead specimens from England and Scotland (Fig. 1). These data show a sharp fall in numbers at ring counts between 70 and 100 years and a long tail-off of older junipers. The maximum count was 192 years for a bush in Upper Teesdale (Gilbert 1980). The ring counts are likely to be underestimates of the true age as it is difficult to be certain of sectioning the trunk at the point where the life of the young seedling is represented. No doubt therefore there are specimens of over 200 years in this country. Elsewhere the maximum age for *J. communis* is an extraordinary specimen from Latvia said to be 2000 years old with a girth of 275 cm (Kanngiesser 1909). A specimen from northern Russia had 544 rings with a diameter of 8·3 cm (girth calculated as 52 cm), and junipers of over 300 years are said not to be infrequent (Kanngiesser 1907). Other species of juniper are also very long-lived, several central Asian species living to be over 1000 years (Mukhamedshin 1977).

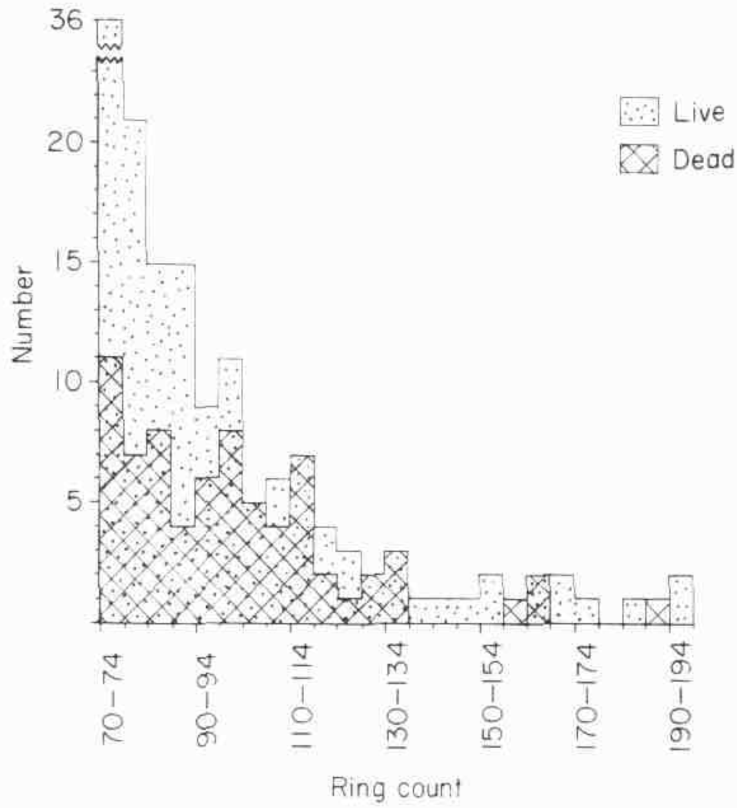

FIG. 1. Ring counts for all known records of living and dead junipers of over 70 years in England and Scotland.

Live and dead junipers both show a steady fall-off in numbers with age (Fig. 1). However, there are fewer dead than live junipers with ring counts of around 70–85. This would be expected if death were commoner after this age.

Ring counts for both the live and dead junipers of southern England have been lower than those from the north of England and from Scotland (Fig. 2). None of all the

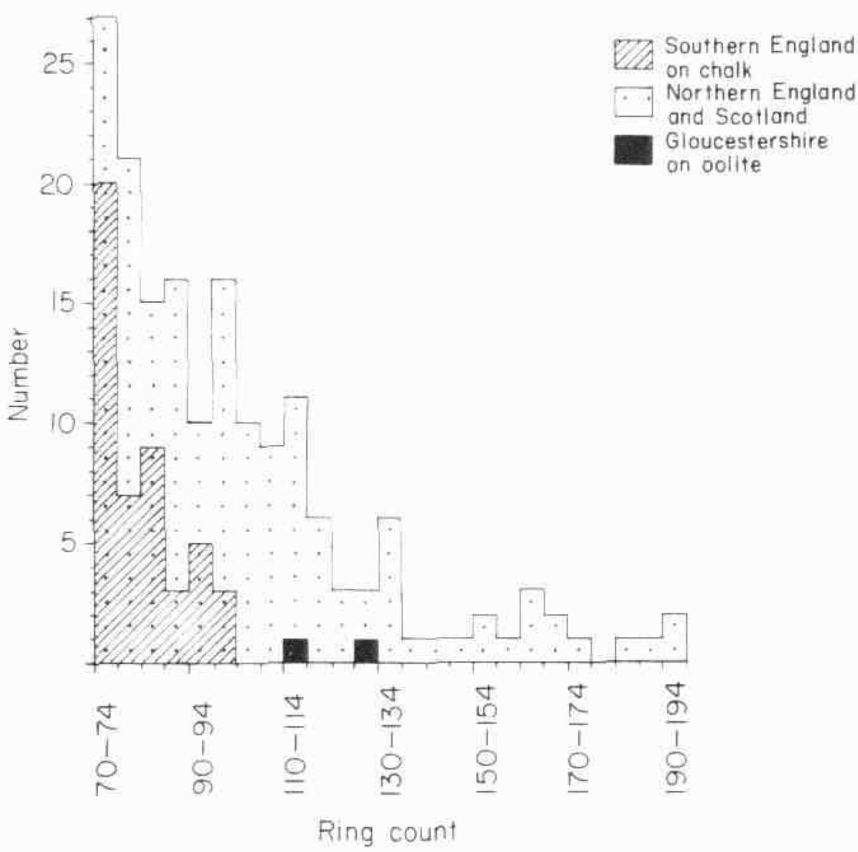

FIG. 2. Ring counts for all known records of junipers of over 70 years showing differences between southern England and northern England and Scotland.

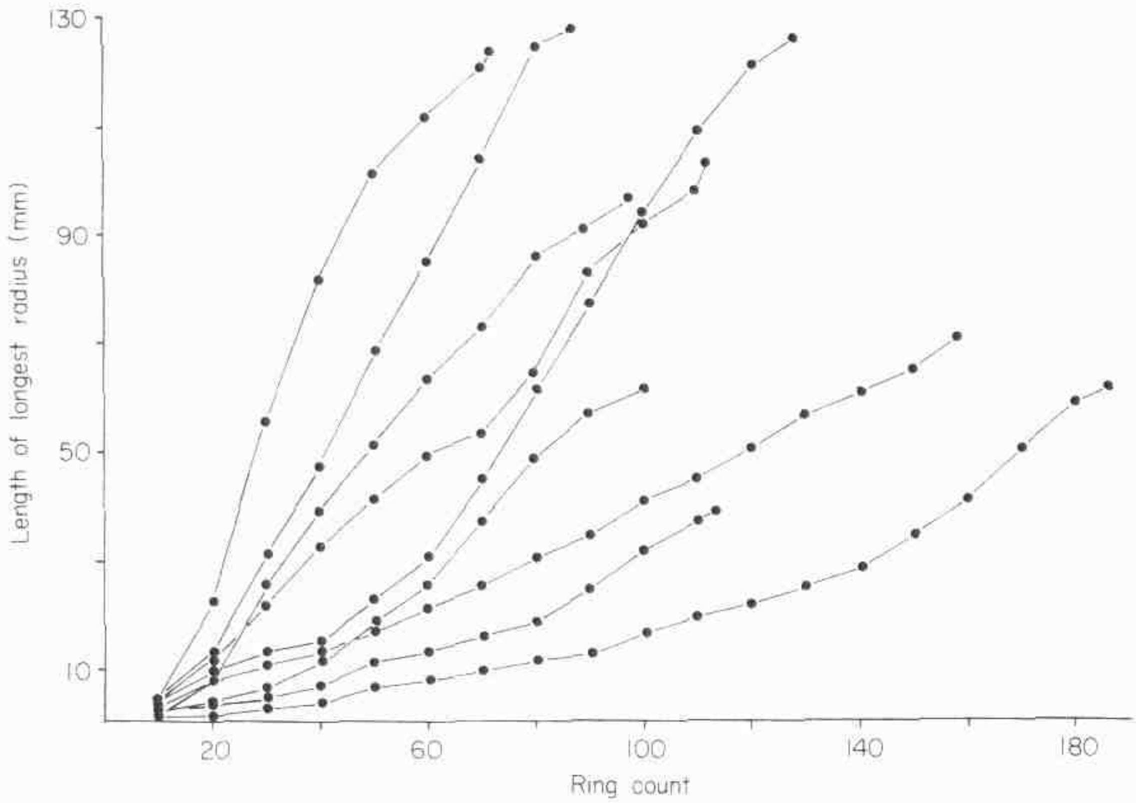

FIG. 3. Some examples of cumulative growth curves shown by dead junipers.

specimens from the southern chalk soils have been recorded with over 100 rings, although three with over ninety-five rings were cut at Porton, Wilts. The specimens with 117 and 128 rings were dead junipers from the oolite of the Cotswolds. Thus, although Whitbarrow in the north and Porton Down in the south both have populations with many dead and dying bushes, the oldest bush in the counts from Porton had ninety-seven rings, whereas at Whitbarrow in Cumbria the oldest bush had 186. Whitbarrow is a much more exposed site with shallow soil and sheep-grazing. The junipers are growing very much slower than at Porton, and unless they are in pockets of deeper soil and sheltered from the wind, reach only about 1 m in height.

Observations of the growth rates and ages of juniper led to the hypothesis that the life-span might be related to the growth rate; slower-growing specimens appearing to live for longer. Growth rates were measured by mean ring widths in 10-year intervals along the longest radius. The slowest growth over the whole life was 0·03 mm per annum for a specimen from Kyloe Crags, Northumberland and the fastest was 1·97 mm from Tynron Juniper Wood, Dumfries. Examples of the variation between some individuals are shown by their cumulative growth curves (Fig. 3). The expected s-shaped growth curve does not show clearly; in particular there is no markedly longer slower growth towards the end of life. This is thought to be partly due to technical difficulties in the measurement of very asymmetric growth. It would be best if the whole area of each ring could be taken into account. Correlations between the mean ring width at 10, 20 and 30 years, before asymmetric growth begins, and the ring count at death were plotted (Fig. 4). The points were scattered for the thirty-six specimens, but there was a significant correlation between $\log_e$ ring count and mean ring width (at 10 years $r = -0{\cdot}397$ $P < 0{\cdot}05$, at 20 years $r = -0{\cdot}357$ $P < 0{\cdot}05$, and at 30 years $r = -0{\cdot}405$ $P < 0{\cdot}02$). The correlation between mean ring width over the entire life and $\log_e$ ring count at death was not significant. An additional twenty specimens where only the mean ring width throughout life was measured were added into the data, but this correlation was not significant either. The reasons for the

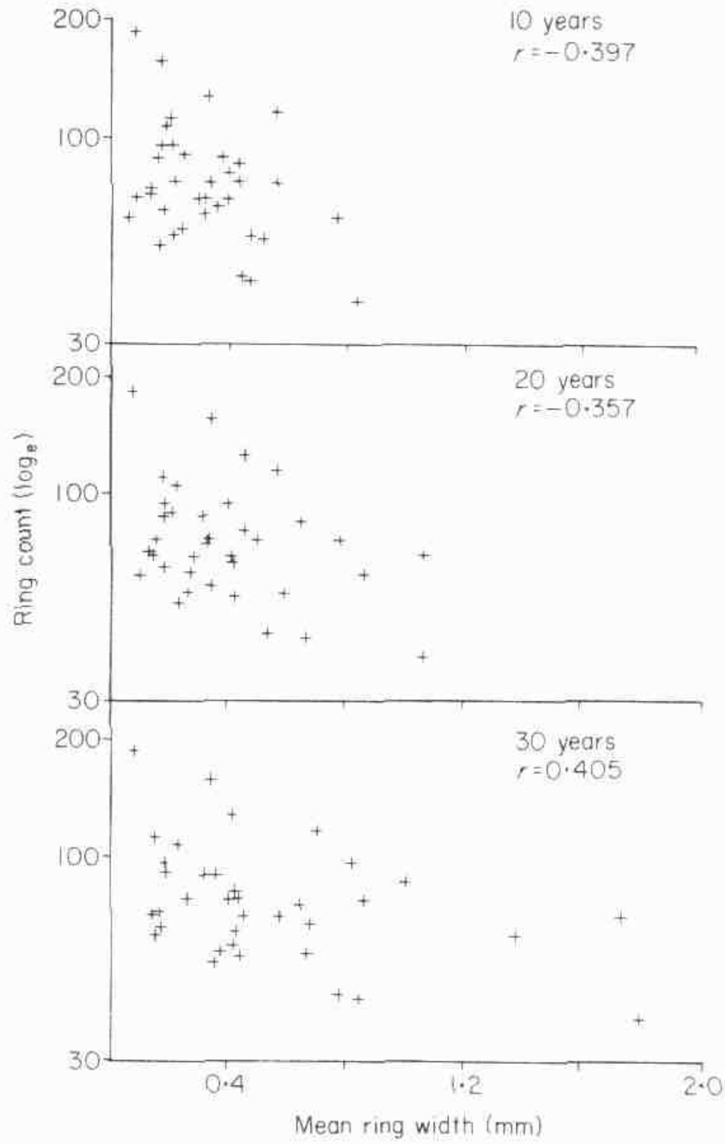

FIG. 4. Correlations between the ring count at death and the mean ring width at 10, 20 and 30 years of age (ring count).

lack of correlation in the overall measurement are not clear. This may be due partly to the growth measure used, but possibly also the effects of the environment on the early years of growth are particularly important in determining the life-span. If early influences are important, then for plants of different ages, the early years have been passed at different calendar times when climatic regimes have varied. Certainly there were some colder periods during the last century, but these are not thought to be important in the present context. When data on living specimens are examined there are no marked discrepancies between the ring counts and growth rates as compared to dead specimens. In general, therefore, the faster-growing plants do not reach the older ages, while slower-growing plants can become old. These slower-growing plants can die at any age, and the great majority of all plants fail to reach the potential ages and growth rates that are shown by exceptional individuals. These exceptions define the limits of the life-span and growth rates of juniper and there are naturally fewer of these because they are less commonly collected. Further studies of juniper, or other species, are needed to fully confirm the relationship of life-span to growth rates.

Size

Size alone is a poor indicator of age in the absence of ring counts, and it is not advisable to draw conclusions about the age of apparently comparable specimens which are growing

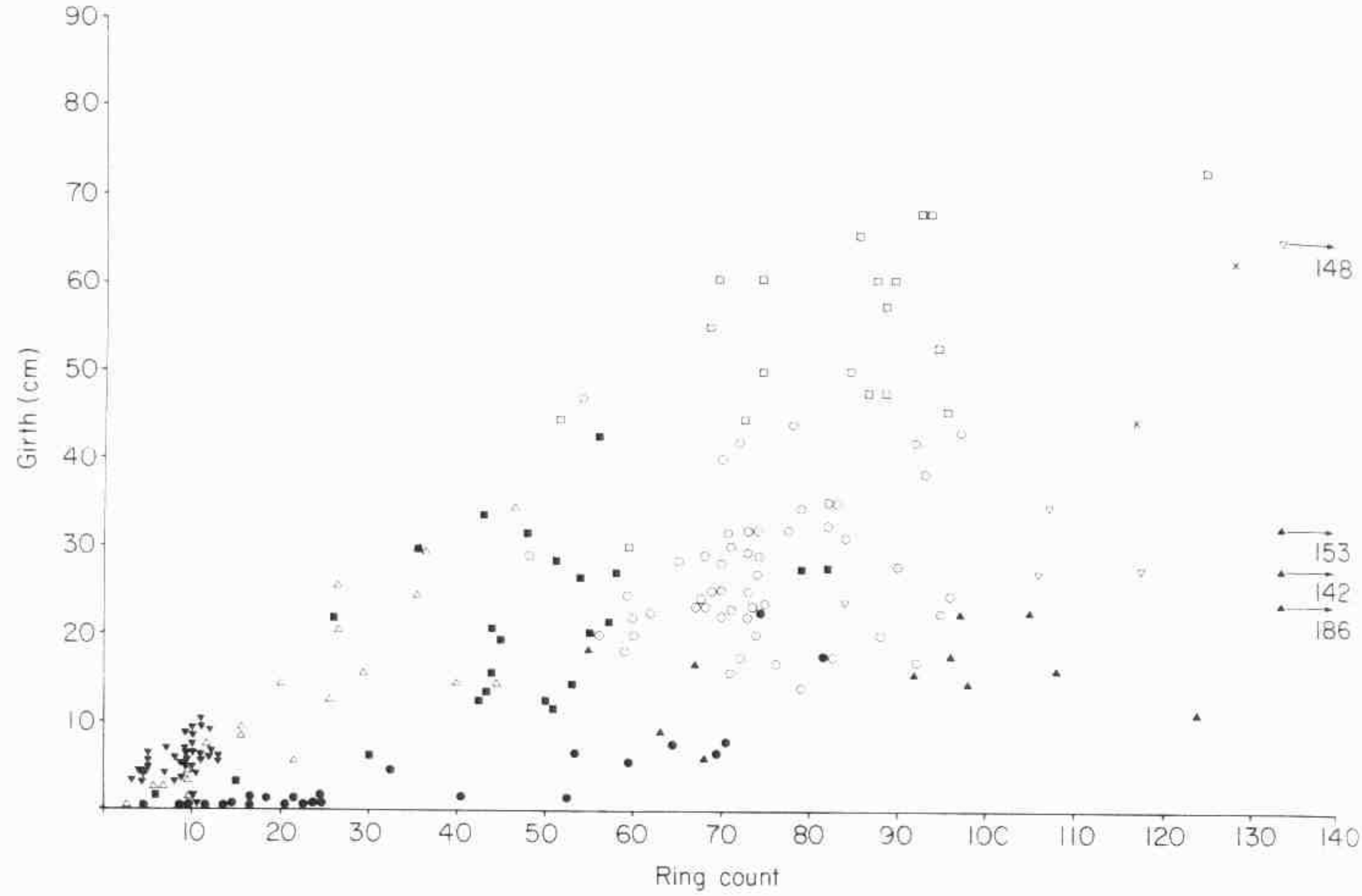

FIG. 5. The relationship between girth and ring count for juniper from nine sites. ▼ young populations at Porton, Hants 1971; ○ old populations at Porton, Wilts 1971; △ Pepper Box Hill, Wilts 1972 (data from Furness, Personal communication); ● Moughton Fell, Lancs from Malins-Smith (1935); ■ Oxenfell, Cumbria 1973; ▲ Whitbarrow, Cumbria 1977 and 1980; × Juniper Hill, Edgeworth Glos. 1974; ▽ The Bog, Northumberland 1973; □ Tynron Juniper Wood NNR, Dumfries, from Kerr (1968).

on different sites. Data for the girth and ring counts of junipers on nine sites show marked variability (Fig. 5). For example, the largest juniper was from Tynron Juniper wood NNR, Dumfries, and had a girth of 82 cm but only eighty-four rings, while the oldest juniper from Whitbarrow had a girth of 20 cm but had 186 rings. Within a site it may be practical to use the regression of ring count on girth to make estimates of the ring counts for uncut bushes, as was done for Oxenfell, Cumbria (Ward 1981). However, this should be done with caution, especially where any field measurements fall outside the range of the cut specimens. The relationship obviously cannot be used at all where there is extreme variation in individuals within a site, as at Whitbarrow. Malins-Smith (1935) thought that some junipers at Moughton Fell were well over 200 years, but he extrapolated from smaller, younger specimens. His largest specimen had a girth of 73·7 cm (estimated to be 180–240 years old), while another was 58·4 cm (estimated as 146–196); but the largest specimen he actually counted rings on had a girth of only 28·7 cm. In 1972, I cut a specimen from this large site (possibly in Malins-Smith's study area) which had a girth of 53·5 cm, but the ring count was only ninety. Thus, Malin-Smith's figures for the age of his older specimens may be overestimates.

Junipers sometimes grow very tall; Elwes & Henry (1912) give details of plants reaching 13 m in height. These are particularly frequent in Scandinavia, and Stormer (1953) records one of 17 m. Junipers of about 9 m grow at Holystone Burn, Northumberland, where ring counts have given ages of up to 120 years. There are large junipers in Scotland, for example, at Crathie Wood, Aberdeenshire. Girth can also be very large, and there are records of trunks of over 2 m (Elwes & Henry 1912). The biggest girth that I have measured was 123 cm for the solitary juniper at Mollen Wood, Bewcastle, Cumbria in 1975.

Reproduction and clonal growth of older junipers

Age affects reproductive output. At Porton, seed samples were examined of sectioned berries from young and old populations of juniper in September 1971. As few as 5·2% of seeds from the older bushes were alive, compared to over 80% in the young bushes (Table 1). Physiological causes related to senescence could be involved in explaining why large numbers of seeds from the older bushes were dead from no immediately apparent cause. In the older bushes also, the rates of attack by insects, mites and fungi were higher than in the younger bushes. Twenty-five per cent of the seeds on old bushes at Roche Court, were affected, while the nearby young bushes had only 0·4% affected (all by *Argyresthia praecocella* Zell.). The higher rates of attack on older bushes are probably related to decreased resistance to the build-up of populations. On other sites, Eriophyiid mites (*Trisetacus quadrisetus* Nal.) can sometimes cause serious damage, especially on older bushes. At Kingley Vale, Sussex in October 1972, for example, eighteen out of twenty-two berries from old bushes were destroyed by these mites. The mites are being studied in more detail for juniper sites on the South Downs by Bristowe (pers. comm.). Seed chalcids, *Megastigmus bipunctatus* (Swed.), can also destroy many seeds. At Chinnor Hill, Oxon, in September 1976, 106 out of 312 seeds examined from old bushes were attacked by this species.

The total production of berries also varies with the life stage of the juniper. Old junipers hardly fruit at all or are completely sterile (Falinski 1980). At Porton between 20% and 60% of the old bushes were sterile (Table 3), and about half of these would be expected to be females.

Clonal growth also occurs. On the dry chalk soils of the south of England it is uncommon, but in northern areas and at high altitudes, expecially in boggy conditions, juniper becomes more prostrate and adventitious roots may be found on buried branches. Vorob'eva (1975) studying the various morphological forms thought that the adventitious roots of the bush form were too weak to prolong the life of the outer branches when the original centre died. Only in the very prostrate forms under severe conditions does the life of the outer ring of branches persist when the original centre dies. Falinski (1980) found that vegetative propagation occurred in the 'condensation' phase of juniper where the older

TABLE 1. Percentage of live and dead seeds in berries from young and old populations of juniper at Porton Down in September 1971

Site	Mean age (ring count)	Live seeds	Dead seeds: Unknown causes	Eriophyiid mites	Fungal attack	Seed* chalcid	Berry† miner	Total seeds examined
Young stands								
Breck	6·5	85·6	14·0	0	0	0·4	0	257
Roche Court	10·3	81·1	18·5	0	0	0	0·4	238
Old stands								
Roche Court	70·9	20·5	54·6	1·4	6·9	5·9	10·9	273
Blakes Firs	75·2	5·2	85·6	3·1	1·9	0·3	3·5	251

* *Megastigmus bipunctatus* (Swed.) (Hym., Torymidae).
† *Argyresthia praecocella* Zell. (Lep., Yponomeutidae).

TABLE 2. Numbers and ratio of females to males and unknown-sex bushes in some young and old juniper populations in southern England

Site and date	Approx. mean age (ring count)	Total	Numbers of junipers: Females	Males	Unknown sex	Ratio of Females : Males : Unknown sex	Notes
Young stands							
Porton, Roche Court, 1971	6·5	100	10	22	68	1·0 : 2·2 : 6·8	Predominantly immature
Porton, Roche Court, 1979	14·5*	78	32	43	3	1·0 : 1·34 : 0·09	Severe rabbit grazing
Porton, Breck, 1971	10·3	96	44	35	17	1·0 : 0·79 : 0·39	
Porton, Breck, 1979	18·3*	63	21	36	6	1·0 : 1·71 : 0·29	Severe rabbit grazing
Bulford, Wilts, 1980	19·0*	111	56	54	1	1·0 : 0·96 : 0·02	
Stockbridge, Hants, 1980	40·0*	98	50	47	1	1·0 : 0·92 : 0·01	
Old stands							
Porton, Roche Court, 1971	70·9*	85	35	43	7	1·0 : 1·23 : 0·2	
Porton, Roche Court, 1979	78·9*	66	19	37	10	1·0 : 1·95 : 0·53	
Porton, Blakes Firs, 1971	75·2	74	23	37	14	1·0 : 1·61 : 0·61	
Porton, Blakes Firs, 1979	83·2*	50	16	27	7	1·0 : 1·69 : 0·44	

* Age estimated (only a few ring counts).

bushes were mixed with young bushes and the scrub became dense and overcrowded. These bushes were not very old however, the maximum age being about 55 years.

Sex ratio in older juniper populations

The sex ratio of juniper populations may not be 1 : 1 (Table 2). In the older populations studied at Porton the males predominated, and this is quite frequent elsewhere in southern England on the chalk. However, it is not always the case, at Bulford the ratio was very close to 1·1, at Stockbridge females predominated slightly, while at Porton Breck in 1971 there were considerably more females at 1 : 0·79 in a young population. Forsberg (1888) recorded variation between populations too, and found some sites where females predominated, as did Falinski (1980) in the older successional phase of a stand in Poland. Forsberg also found that males were more frequent than females on sites with drier nutrient-poor soils, while Falinski (1980) found a similar phenomenon within his study site. Old remnant junipers of formerly important sites in England seem to be male plants more frequently than female, although statistical evidence for this is not yet available. Examples of such sites are Park Downs, Surrey, Bix Bottom, Oxon, and Waskerley Beck, Durham. Forsberg (1888) also thought that males tended to live longer than females. It is probable that the female bushes are more frequently sterile than the males in older stands. Generally in flowering plants, the reproductive output in seed production by females is greater than pollen production by males, and consequently the sexes may be expected to suffer differential mortality (Freeman, Klikoff & Harper 1976). This is thought to account for the topographic difference in occurrence of males and females on the Polish site (Falinski 1980).

The past history of a site may also be important in attempting to explain unequal sex ratios. On the first of two visits to Porton, the young junipers were not fully mature, and males appeared to predominate on Roche Court because they begin to flower slightly earlier than females which were mostly immature (Table 2). On Porton Breck, where the bushes were slightly older, the females exceeded the males by 1·0 : 0·79. Eight years later however the ratio of the sexes of this latter population had changed strongly in favour of males at 1·0 : 1·71. In the intervening years severe grazing by rabbits occurred causing serious mortality of the junipers; at Porton Breck 3% were recorded as dead in 1971, but this rose to 37% by 1979. Of the many deaths, it seems that more females died. This does not appear to have occurred on a nearby site of similar age, Bulford Downs, where there has been little or no rabbit-grazing or mortality of juniper. Here the ratio of females to males is near parity at 1·0 : 0·963. Thus periods of severe grazing may have occurred in the past and affected stands which are still present today.

Senescent populations

Some juniper populations have many dead and dying bushes. This may not always be connected with longevity, since, for example, shading causes the death of bushes under the dense tree canopies that can develop during secondary succession. Juniper does not normally survive under yew (*Taxus baccata* L.) or beech (*Fagus sylvatica* L.), although it persists in glades or under the light shade of trees such as birch (*Betula* spp.). Regeneration does not usually occur under these conditions. Damage and death may be caused by fire or by grazing. The effects of intensive rabbit grazing on young bushes were discussed briefly in Ward (1981).

Other, older, juniper populations however may have many dead and dying bushes which are neither shaded, heavily grazed nor damaged. These moribund bushes have partly or entirely dead branches or twigs, failure or reduction of flowering or fruiting, very slow incremental annual growth of shoots, and discoloured foliage. Various causes such as changing climate (Grose 1957), sulphur dioxide pollution (Bowen 1965) and soil erosion (Hope-Simpson 1957) have been suggested to account for these declining populations, but it is very likely that the natural senescence of juniper is involved. Bushes may appear to have died simultaneously in these populations, but this is a false impression created by their resistence to rotting. Some specimens may have died more than 10 years earlier. The numbers that died in the previous year are shown by counting individuals which still have most of their needles, as these usually fall off by the second season after death. Statistics for the live, moribund and dead bushes of some old stands are given in Table 3. At Porton Blakes Firs, for example, 25% of the bushes were dead in 1971, rising to some 50% in 1979. At the second count 3% of the bushes had died in the previous year and 9% were moribund.

If the future of these old juniper populations is to be predicted, then their demography needs to be known. This has not been done in sufficient detail for any stand in this country, although Ward (1981) described age structure of typical stands. Falinski (1980) studied an interesting population in Poland where regeneration has continued through to the generation following the pioneer juniper. This does not usually occur in England, most lowland stands have an initial flush of colonization lasting for a variable number of years, and then there is usually no further regeneration within the stand. Nearby areas where conditions are suitable are colonized. Under certain special circumstances regeneration may continue resulting in stands with all ages of bushes. This is usually where the vegetation remains open continuously, e.g., in eroded areas, such as quarries, and perhaps under certain grazing regimes. For the Porton, Blakes Firs site in 1971 the age range was 54–97 years (ring counts of twenty specimens) and the mean age was $72{\cdot}5 \pm 11{\cdot}4$ (Table 3). It can be predicted therefore that this population will not be present at all in 50 years time if the juniper lives to only about 100 years on this southern chalk site. The population will be severely depleted before this, indeed, it has already reached 50% dead. Whitbarrow however, has a much bigger age range, and the juniper has been found to live for longer on this exposed northern site. Thus, although there are already quite a high proportion of dead and dying bushes on this site, we can predict that at least some of the juniper will persist on this site for 100 years, even in the absence of regeneration.

TABLE 3. Counts of numbers of live, moribund and dead junipers in some older populations

Site	Live	Dead	Moribund	Dead + needles	Total	Ring count Mean	Ring count Range
Lodge Hill, Bucks 1974	48	61	39	3	109	59*	45–79
Beacon Hill, Aston Rowant NNR, Oxon 1974	52	53	20	5	105	74*	57–90
Porton, Roche Court, 1971	85	15	7	—	100	71*	48–97
Porton, Roche Court, 1979	66	34	8	1	100	—	—
Porton, Blakes Firs, 1971	74	25	8	—	99	75	54–96
Porton, Blakes Firs, 1979	50	50	9	3	100	—	—
Whitbarrow, Cumbria 1980	60	42	25	—	102	102*	55–186

Ring counts from samples of 10–20 trunks.
—Not counted.
* Dead specimens used in ring counts.

DISCUSSION

The intrinsic life-span of juniper is believed to be of major importance in explaining why old unshaded bushes are often found dying or dead. Exceptional individuals reach ages nearing 200 years in Britain, and slowing growth and increasing sterility in the older bushes points to the involvement of physiological factors related to senescence. Junipers die of age-related disorders or diseases, such as basal rots and cankers, and attacks by insects and mites also increase with age. Wind-throw may be related to age also as old large upright junipers are more likely to be affected by severe winds, especially if their root systems are weakening. Further work on the reasons for mortality of old bushes and their relationship to the physiological state of the plants is needed.

There are considerable variations within and between juniper populations in growth rates and life-span. The life-span itself seems to vary in relation to growth conditions. The faster-growing specimens of southern England reach a span of over 100 years only in exceptional cases, while in the north of England and at higher altitudes where growth is slower juniper can apparently live for longer and bushes near to 200 years are found. For *Pinus sylvestris* also life-span is said to be prolonged by poor growth (Backman 1943), and slow metabolism is found in some long-lived plants (Molisch 1938). Environmental influences have been shown to be important in the early years of growth of juniper in relation to later life-span. In other fields of work there are also suggestions that this might be relevant, thus, there is thought to be a relationship between age at which sexual maturity occurs and life-span; plant species which take longer to their first flowering living for longer (Molisch 1938; Backman 1943). In the cloning of spruce from cuttings, problems of poor growth are encountered when cuttings are taken from older plants. This growth pattern is not fixed in younger stock (Roulund 1981). We can speculate further, that anywhere where growth is slower, as for example, on the edge of the range of a plant species, longevity might be increased; this was noted for some shrubs by Kanngiesser (1907). Slower growth could also be a cause of male junipers living far longer than females, as males are said to grow in drier and more nutrient-poor situations than females. The life of bushes may also be prolonged where adventitious roots are present on buried branches (Kanngiesser 1907).

Woolhouse (1972) suggested that the overall pattern of survival of woody plants is often represented by an 'ecological survival curve' where chance factors account for mortality. This type of curve is like that of the present data on juniper (Fig. 1), although this shows greater mortality at around 85 years, which may indicate the rising importance of senescence. Clearer evidence of limited life-span might be obtained by studying single senescent populations in much more detail, not by lumping data from many variable populations.

Where the conservation of juniper on particular sites is concerned, the age structure of the populations needs to be assessed before any prediction of the future can be made. Some idea can be obtained by examining the age and growth rates of the dead bushes. Stands may have only limited age classes, and there may be only tens of years before severe depletion of the bushes can be expected. For example, the stand on Beacon Hill at Aston Rowant NNR has 50% dead bushes now, many live bushes are unhealthy (Table 3) and the bushes can be expected to be almost all dead within 50 years. The stand of fine old bushes at Tynron Juniper Wood, NNR in Dumfries is thought to be in the early stages of the senescent phase. The difficulties of promoting regeneration steadily increase as the older bushes die off leaving fewer seed parents, which themselves are becoming less successful in producing seeds. Unfortunately, the study of management methods for regeneration is only in its early stages, and we are not yet in a position to suggest the best means of producing new juniper stands (Ward 1981).

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