Annals of Botany **106**: 859–870, 2010
doi:10.1093/aob/mcq191, available online at www.aob.oxfordjournals.org

ANNALS OF BOTANY
Founded 1887

REVIEW

Longevity of clonal plants: why it matters and how to measure it

Lucienne C. de Witte* and Jürg Stöcklin

Section of Plant Ecology, Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland
** For correspondence. E-mail Lucienne.dewitte@unibas.ch*

Received: 23 March 2010 Returned for revision: 16 July 2010 Accepted: 25 August 2010 Published electronically: 29 September 2010

• *Background* Species' life-history and population dynamics are strongly shaped by the longevity of individuals, but life span is one of the least accessible demographic traits, particularly in clonal plants. Continuous vegetative reproduction of genets enables persistence despite low or no sexual reproduction, affecting genet turnover rates and population stability. Therefore, the longevity of clonal plants is of considerable biological interest, but remains relatively poorly known.
• *Scope* Here, we critically review the present knowledge on the longevity of clonal plants and discuss its importance for population persistence. Direct life-span measurements such as growth-ring analysis in woody plants are relatively easy to take, although, for many clonal plants, these methods are not adequate due to the variable growth pattern of ramets and difficult genet identification. Recently, indirect methods have been introduced in which genet size and annual shoot increments are used to estimate genet age. These methods, often based on molecular techniques, allow the investigation of genet size and age structure of whole populations, a crucial issue for understanding their viability and persistence. However, indirect estimates of clonal longevity are impeded because the process of ageing in clonal plants is still poorly understood and because their size and age are not always well correlated. Alternative estimators for genet life span such as somatic mutations have recently been suggested.
• *Conclusions* Empirical knowledge on the longevity of clonal species has increased considerably in the last few years. Maximum age estimates are an indicator of population persistence, but are not sufficient to evaluate turnover rates and the ability of long-lived clonal plants to enhance community stability and ecosystem resilience. In order to understand the dynamics of populations it will be necessary to measure genet size and age structure, not only life spans of single individuals, and to use such data for modelling of genet dynamics.

Key words: Age, community stability, genet size, global change, life history, population dynamics, somatic mutation, vegetative reproduction.

INTRODUCTION

The life span of plants, as in any other organism, is a key demographic trait for understanding life history (Weiher *et al.*, 1999), population dynamics (Harper, 1977; Silvertown and Lovett Doust, 1993) and evolutionary fitness (Silvertown, 1991). Extended longevity of plants is believed to enlarge persistence of populations and thus affects community stability and vegetation responses to present and future climate change (Steinger *et al.*, 1996; Eriksson, 2000; Körner, 2003; García *et al.*, 2008; Morris *et al.*, 2008). Unfortunately, there are few reliable data on genet longevity and genet turnover rates in plants, because these are difficult to measure (Dietz and Schweingruber, 2002). Known maximum longevity ranges from a few weeks in annuals (e.g. Bliss, 1971; Sharitz and McCormick, 1973) to thousands of years in some clonal herbs and trees (Table 1; e.g. Wherry, 1972; Lynch *et al.*, 1998; Brundu *et al.*, 2008). This wide variation seems to be due to trade-offs between life span and other fitness traits and because the modular construction of plants and their indeterminate growth counteract intrinsic senescence. The broad range in longevity also implies that there are considerable differences in the timescale of population dynamics and in the selective forces acting on individual plants.

In clonal plants, temporal gaps between years with successful sexual recruitment were found to be highly variable in length, from zero to thousands of years (Eriksson, 1989). For example, in high alpine meadows, sexual reproduction can be hampered due to a lack of pollinators or from low temperatures that inhibit seed germination. In such habitats, clonality can enhance genet longevity considerably, it can compensate for the partial loss of genets due to disturbance, and thereby it can secure population persistence for long periods of time. In general, clonal reproduction allows plants to benefit from a potential two-fold fitness, persistence of the product of a single zygote plus repeated economical offspring production (Aarssen, 2008).

Persistent clonal reproduction of an individual not only enhances longevity, but it can also lead to genets inhabiting large areas, because clonal plants have a pronounced capacity to spread horizontally (Stöcklin, 1992; Herben and Hara, 1997; Hutchings and Wijesinghe, 1997). Therefore, many studies use size and annual size increments of a genet to measure its age (e.g. Vasek, 1980; Steinger *et al.*, 1996; Reusch *et al.*, 1998; Wesche *et al.*, 2005), although size and age are not always linearly correlated. It is important to note that longevity of a genet is independent of ramet life span, and thus the spatial structure of all ramets belonging to the same genet is only an incomplete mirror of the life history of the entire genet. When genets become fragmented and when annual growth increments indicate high interannual variability, the relationship between size and age becomes particularly weak.

TABLE 1. *Size (usually diameter) and longevity (in years) of clonal plants from the literature, separated into trees, shrubs, herbs, grasses, other species, and with an indication of the method used for size or age determination*

(a) Clonal trees

	Method to estimate the size of the clone	Size of clone [diameter (m, or as indicated)]	Estimated age of oldest genet (years)	Estimated age of youngest genet (years)	Reference(s)
Olea europaea subsp. *laperrinei*	Molecular markers	80 m^2 +	1000 +	–	Baali-Cherif and Besnard (2005)
Picea abies	Radiocarbon dating	–	10 000 –12 000	–	Kullman (2008)
Picea mariana	Morphological and growth ring analysis, statistical analysis	14	300	–	Legère and Payette (1981)
	Molecular markers and dendrochronological analysis	691·3 m^2	1800 +	100	Laberge *et al.* (2000)
Pinus longaeva	Growth ring analysis	–	4900	–	Schulman (1958), Johnson and Johnson (1978), Brown (1996)
Populus alba	Molecular markers	–	>12 000	–	Brundu *et al.* (2008)
Populus tremuloides	Morphological analysis, aerial photographs	510	10 000 +	–	Kemperman and Barnes (1976)
	Microsatellite divergence based on mutation accumulation	–	12 000	14	Ally *et al.* (2008)
Populus tremula	Molecular markers	16	152	2	Suvanto and Latva-Karjanmaa (2005)
Ulmus procera	Molecular markers and microsatellite divergence based on mutation accumulation	–	2000	–	Gil *et al.* (2004)

(b) Clonal shrubs

	Method to estimate the size of the clone	Size of genet [diameter (m, or as indicated)]	Annual growth rate (cm $year^{-1}$)	Estimated age of oldest genet (years)	Estimated age of youngest genet (years)	Reference(s)
Arctostaphylos alpina	Growth ring analysis	–	–	93	–	Schweingruber and Poschlod (2005)
Calluna vulgaris	Growth ring analysis	–	–	58	–	Mork (1946)
Dryas octopetala	Growth ring analysis	–	–	108	–	Kihlman (1890)
Empetrum nigrum ssp. *nigrum*	Growth ring analysis	–	–	140	–	Bell and Tallis (1973)
Erica carnea	Growth ring analysis	–	–	82	–	Schweingruber and Poschlod (2005)
Juniperus sabina	Growth ring analysis	–	–	67–70	–	Molisch (1929)
	Molecular markers	795 m^2	1·8–6·8	770–2940	–	Wesche *et al.* (2005)
Larrea tridentata	Molecular markers, growth rings, radiocarbon dating	16·6	–	11 700	–	Vasek (1980)
	Growth rings, radiocarbon dating	11	–	9170	–	Vasek (1980)
Loiseleuria procumbens	Growth ring analysis	–	–	110	–	Schweingruber and Poschlod (2005)
Lomatia tasmanica	Molecular markers, chromosome counts and radiocarbon dating	1200	–	43 600	–	Lynch *et al.* (1998)
Rhododendron ferrugineum	Growth ring analysis	–	–	202	–	Schweingruber and Poschlod (2005)
	Molecular markers	20 m^2	2·6	300	–	Escaravage *et al.* (1998)
	Molecular markers	25 m^2	115	283 +	28	Pornon *et al.* (2000)
Salix arctica	Growth ring analysis	–	–	150	–	Kraus (1873)
Vaccinium vitis-idaea	Growth ring analysis	–	–	109	–	Callaghan (1973)

(c) Clonal herbs (except grasses and sedges)

	Method to estimate the size of the genet	Size of genet [diameter (m, or as indicated)]	Annual growth rate (cm year^{-1})	Estimated age of oldest genet (years)	Reference
Acantholimon diapensoides	?	–	–	400	Agakhanyantz and Lopatin (1978)
Anemone nemorosa	Growth ring analysis	–	–	>5	Shirreffs (1985)
	Molecular markers	12	1·9–3·1	190–320	Stehlik and Holderegger (2000)
Calamagrostis epigejos	Comparative analysis of site history and genet size	50	–	400	Oinonen (1969)
Convallaria majalis	Comparative analysis of site history and genet size	850	–	670 +	Oinonen (1969)
Cypripedium calceolus	Molecular markers	39 ramets	1–1·5	370	Brzosko *et al.* (2002)
Gaylusaccia brachycerium	Morphological analysis	1980	–	13 000 +	Wherry (1972)
Silene acaulis	Growth ring analysis	–	–	252	McCarthy (1992)
	Modelling: size-based population projection matrices	>0·2	–	300 +	Morris and Doak (1998)
Teucrium scorodonia	Morphological analysis	Several square metres	–	50–100	Hutchinson (1968)
Trifolium alpinum	Growth ring analysis	–	–	50	Schweingruber and Poschlod (2005)

(d) Clonal grasses and sedges

	Method to estimate the size of the genet	Size of genet [diameter (m, or as indicated)]	Annual growth rate (cm year^{-1})	Estimated age of oldest genet (years)	Reference
Calamagrostis epigejos	Comparative analysis of site history and genet size	50	–	400 +	Oinonen (1969)
Carex curvula	Molecular markers	1·6	0·04	2000	Steinger *et al.* (1996)
Carex ensifolia ssp. *arctisibirica*	Molecular markers	40	–	3800 +	Jónsdóttir *et al.* (2000)
Carex stans	Molecular markers	7·4	–	Approx. 150	Jónsdóttir *et al.* (2000)
Festuca ovina	Morphological analysis, cross-pollination tests	8·25	0·3	1000 +	Harberd (1962)
Festuca rubra	Morphological analysis, cross-pollination tests	220	22·9	1000 +	Harberd (1961)
Holcus mollis	Morphological and phenological analysis, chromosome analysis	880	–	1000 +	Harberd (1967)
Sasa senanensis	Molecular markers	300	Approx. 100	Several decades	Suyama *et al.* (2000)
Stipa pennata	Calendar age determination (Gatsuk *et al.*, 1980)	–	–	75	Vorontzova and Zaugolnova (1985)

(e) Clonal pteridophytes and marine species

	Method to estimate the size of the genet	Size of genet [diameter (m, or as indicated)]	Annual growth rate (cm year^{-1})	Estimated age of oldest genet (years)	Reference
Lycopodium annotinum	Comparative analysis of site history and genet size	Up to 250	–	250	Oinonen (1967)
	Morphological analysis	–	–	21	Callaghan (1980)
	Molecular markers	36	20	90 +	Wittig *et al.* (2007)
Lycopodium comoplanatum	Comparative analysis of site history and genet size	250	–	850	Oinonen (1969)
Pteridium aquilinum	Comparative analysis of site history and genet size	489	–	1400	Oinonen (1967)
	Molecular markers	1015	43	1180	Parks and Werth (1993)
Zostera marina	Molecular markers	33	13	134	Reusch *et al.* (1998)

Methods include growth ring analysis, morphological analysis, radiocarbon dating, comparative analysis of site history, molecular markers and microsatellite divergence (see text for more explanation).

With this in mind, genet age seems to be difficult to measure, even when the spatial extension of a genet is known. Nevertheless, there have been many attempts to measure maximum longevity in clonal plants, either for curiosity or because it can serve as an indicator of population persistence.

Currently, there is considerable effort to find alternative methods to estimate longevity that are not based on genet size. For example, molecular divergence based on somatic mutations and cell-growth estimates (Ally *et al.*, 2008) or the proportion of ramets to genets (variation due to somatic mutation vs. recombination; Mock *et al.*, 2008) are being used. Also stage-based population or transition-matrix models can be useful tools to investigate life history, dynamics and individual longevity (Ehrlén and Lehtilä, 2002).

Here we critically review the present knowledge on genet longevity in clonal plants, which ranges from a few months up to several thousand years. We summarize and discuss the methods that have been used to estimate genet age and we examine their suitability. A comprehensive overview of published life-span data for clonal trees, shrubs, herbs and grasses is presented in Table 1. Next to the discussion on the recent progress in genet life-span determination and its importance, we examine the literature on the topic of somatic mutations and the role of genet longevity for population dynamics and community stability.

MAXIMUM LONGEVITY OF CLONAL TREES, SHRUBS, HERBS AND GRASSES

Genet life span, a fundamental aspect for understanding life history, is one of the highly attractive but least accessible traits in plants (Dietz and Schweingruber, 2002). Measurements of life span in plants that goes beyond the simple classification into annuals, biennials and perennials is available primarily for trees, in which counting the annual growth rings is a convenient and direct way to determine age (Ehrlén and Lehtilä, 2002). With dendrochronology the 'oldest living tree' was found in Nevada, USA, a bristlecone pine (*Pinus longaeva)* about 4800 years old (Schulman, 1958; Brown, 1996; Lanner and Connor, 2001). For trees that are able to reproduce clonally, genet longevity was found to exceed the maximum age of single tree stems considerably. With dendrochronological analysis, an age of about 300 years was determined for a *Picea mariana* tree in 1981 (Legère and Payette, 1981; Table 1c). Twenty years later, using molecular markers, a genet of the same species consisting of several stems was estimated to be more than 1800 years old (Laberge *et al.*, 2000). Genets of *Populus tremuloides* were found to form large forest patches up to 80 ha based on morphological analyses and analyses of aerial photographs. From this, an estimated longevity of 10 000 years has been suggested by Kemperman and Barnes (1976). Analysis of microsatellite divergence based on mutation accumulation about 30 years later revealed an age of 12 000 years for this species (Ally *et al.*, 2008). Radiocarbon dating applied to fossil wood resulted in extreme life-span estimates for several clonal species (e.g. *Picea abies*, Kullman, 2008; *Lomatia tasmanica*, Lynch *et al.*, 1998).

Genet age of non-trees has long been ignored in the literature, for example in biological floras (but see Poschlod *et al.*, 1996). Only in the second half of the 20th century did researchers start to determine the life span of shrubs, herbs and grasses. Direct measurements of morphological structures, such as via herbchronology, usually account for maximum ages of only a few decades, for example 50 years for the clonal herb *Trifolium alpinum* (Schweingruber and Poschlod, 2005; Table 1c). With more recent methods, which will be described below, longer genet life spans have been reported in shrubs, herbs and grasses (e.g. Escaravage *et al.*, 1998; Stehlik and Holderegger, 2000; Wesche *et al.*, 2005), indicating that these life forms can reach maximum ages of one to several hundreds of years and, in some cases, thousand years (Table 1b–e). Hence, there is no indication from the available literature that genets of shrubs, herbs or grasses have potentially lower life spans than trees, but plant life forms of shrubs, herbs and grasses that can be safely attributed to a single genet are usually much younger than the massive outliving stems of trees.

Maximum age estimates may be in part a product of curiosity. Scientifically, they are an indication of the slowest possible genet turnover rate in a population. Moreover, they tell us more about adult survival relevant for an understanding of the life history and demography of a species (Silvertown *et al.*, 1993; Franco and Silvertown, 1996). However, the maximum longevity ever recorded for a species depends on the sampling effort taken and of the methods used, making it difficult to compare the data.

METHODS TO MEASURE LIFE SPAN IN PLANTS

Direct methods

The following direct methods have been used to determine the life span of clonal plants. (1) Analysis of annual growth rings, a widely used method usually applied to stems of trees, can also be applied to herbs and shrubs that have primary root systems or woody stems with visible growth rings (herbchronology; Zoller, 1949; Dietz and Ullmann, 1997; Schweingruber and Dietz, 2001; Dietz and Fattorini, 2002). Schweingruber and Poschlod (2005) determined the life span of many species with this method and included a critical evaluation of the method. Growth ring analysis is relatively quick, and makes comparisons among successional stages or ecosystems easily possible (Dietz and Ullmann, 1998; Kuen and Erschbamer, 2002; Erschbamer and Retter, 2004; Jónsson, 2004; Von Arx and Dietz, 2005; Perkins and Parks, 2006; Kuss *et al.*, 2008). With this method, for example, it was found that *Vaccinium myrtillus* ramets were significantly younger on ski pistes in the Swiss Alps than in control plots (Rixen *et al.*, 2004). (2) Radiocarbon (C^{14}) dating is usually applied to organic remains of archaeological sites (e.g. Vasek, 1980; Kullman, 2008), but is relatively expensive. These first two methods are only reliable for clonal plants when the oldest parts of the genet are still in place and can be identified. Another disadvantage is that these two methods normally result in single age estimates not useful for population demographic analysis. (3) Growth-form or phenological analysis based on annual morphological markers (e.g. Troll, 1937; Harberd, 1967; Kemperman and Barnes, 1976; Kull and Kull, 1991; García and Antor, 1995;

Jäger *et al.*, 1997) is used to study growth strategies, age-related patterns, size and age distribution or survivorship curves. By counting annual growth increments, Callaghan (1980) estimated an age of 21 years for a genet of the clonal plant *Lycopodium annotinum* (Table 1e). (4) Permanent plot research involves long-lasting research efforts, but yields highly reliable age determinations (e.g. Bärlocher *et al.*, 2000; Erschbamer and Winkler, 2005). This method is especially appropriate for use in geophytes, such as orchids, which may disappear from above ground for years (Tamm, 1948, 1956; Inghe and Tamm, 1985). (5) Age determination by colour band analysis in grasstrees allows for the reconstruction of fire history (Ward *et al.*, 2001; Colangelo *et al.*, 2002). Less known and seldomly applied methods include (6) comparative analysis of site history (Oinonen, 1967), (7) age state determination (Rabotnov, 1950; Gatsuk *et al.*, 1980; Kawano, 1985; Vorontzova and Zaugolnova, 1985) and (8) chromosome analysis (Harberd, 1967).

Only rarely has a life span longer than 200 years been found with the above listed direct methods (Table 1). The main drawback is that only surviving and connected plant structures can be measured and attributed, with certainty, to a particular genet. Therefore, direct measurements systematically underestimate the longevity of clonal plants.

Indirect estimates of age

The size or diameter of a genet can be divided by a measure of mean annual size increment (Suvanto and Latva-Karjanmaa, 2005), yielding an indirect estimate of its age. Several maximum age estimates are based on this method (e.g. Steinger *et al.*, 1996; Reusch *et al.*, 1998). Clonal plants covering large areas can intermingle with other genets and the longer they survive, the more likely they are to become fragmented or to partially die. This hampers easy recognition of entire genets by eye. To overcome these difficulties, some scientists have used genet-specific morphological markers or self-incompatibility tests to detect the size of genets and to determine their age. Harberd (1962, 1967; Table 1d), for example, reported extremely large sizes and old ages for *Festuca rubra* (diameter 220 m) and *Holcus mollis* (880 m) based on self-incompatibility tests. Barsoum *et al.* (2004) identified genets by excavation of root connections, but this method is strongly invasive and causes biases when roots graft naturally or connections are lost over time. Today, the use of DNA fingerprinting techniques, discussed further below, facilitates precise genet identification.

The accuracy of such indirect age estimates largely depends on the reliability of the annual size increment measurement. Size increments can be highly variable among individuals depending on ontogenetic development, successional stage, competitive and nutritional conditions, and environmental factors. The larger and older a genet is, the more critical it is to estimate its expansion rate over the entire life span. Age estimates are therefore generally less accurate than estimates of genet size, and also because the relationship between size and age is not always linear in clonal plants. Therefore, age estimates of genets should include such putative variation, but this is rarely the case (but see Vasek, 1980).

The use of DNA fingerprinting

Although the methods used to measure the size of clonal plants, discussed above, may be doubtful or might not recognize the total size of large genets, modern molecular analysis of leaf samples now allows for a better identification of entire genets. In recent decades, genet identity has been revealed by genetic markers such as allozymes (e.g. Stehlik and Holderegger, 2000) and DNA fingerprinting techniques such as microsatellites (e.g. Suvanto and Latva-Karjanmaa, 2005), random amplification of polymorphic DNAs (e.g. Laberge *et al.*, 2000) or amplified fragment length polymorphisms (e.g. Escaravage *et al.*, 1998). With molecular markers, individuals can be distinguished, allowing spatially explicit sampled plant material to be assigned to genets. Based on the use of a defined sampling distance, genet size can be determined and then divided by a measure of annual growth increment to obtain age information. Using DNA fingerprinting, the oldest genet occurring in a population of the alpine clonal dwarf shrub *Rhododendron ferrugineum* was estimated to be 300 years (Escaravage *et al.*, 1998; Table 1b) and a genet of the alpine grassland species *Carex curvula* was found to be an estimated 2000 years old (Steinger *et al.*, 1996; Table 1d).

The use of DNA fingerprinting techniques has the advantage that a large number of markers can be developed easily and at low cost (Jones *et al.*, 1997; Mueller and Wolfenbarger, 1999). Further advantages include the possibility to sample over large spatial scales and that it causes minimal impact on populations. Unfortunately, there is still some ambiguity associated with two types of molecular assignment errors: misidentification of genetically similar ramets as one genet and misidentification of dissimilar fingerprints as genetically distinct individuals (Widen *et al.*, 1994). Repeated samples coming from the same genet but from different ramets do not always have identical fingerprints. This may result from somatic mutations, from contamination in the laboratory, or from scoring errors that may happen during data analysis (Arens *et al.*, 1998; van der Hulst *et al.*, 2000; Douhovnikoff and Dodd, 2003). Bias introduced by scoring errors has been underestimated until recently (Pompanon *et al.*, 2005; Arnaud-Haond *et al.*, 2007; Bonin *et al.*, 2007), but it is now accepted how crucial it is to apply repeatability tests and statistical tools to critically evaluate error probability in molecular fingerprinting studies (Lasso, 2008).

In crop science, DNA fingerprinting has achieved importance because this technique is used to identify genetic relationships between cultivars and establishes pedigree reconstructions. Thereby, the life span of several cultivars was revealed, for example grapes (*Vitis vinifera*). For the clonally propagated and economically important grapevine cultivar ‘Albarino’, from north-western Spain, which is being used in a recent breeding programme, was given an estimated age of 200–300 years (Alonso *et al.*, 2007). ‘Rouge du Pays’, presently cultivated in the Valais (Switzerland), was already mentioned in a manuscript from the year 1313 (Vouillamoz *et al.*, 2003), suggesting an even longer life expectancy for grapevine cultivars.

The crop plant vanilla (*Vanilla planifolia*) is propagated only vegetatively in many areas due to a lack of pollinators. On islands in the Indian Ocean, where the plants have been

cultivated since the early 1800s, almost all accessions were found to constitute a single and probably very old genet (Bory *et al.*, 2008; Lubinsky *et al.*, 2008).

Overall, molecular size determination in clonal plants has led to better insights into population size and age structure owing to the extensive and qualitative genet detection. However, its accuracy can be impaired by genetic assignment errors due to somatic mutations and scoring mistakes. Therefore, efforts to improve the molecular assignement are necessary for reliable results.

Demographic approaches to longevity

Increasingly, studies are using size- or stage-structured matrix models to estimate demographic properties of long-lived plants (Callaghan, 1976; Erschbamer, 1994; Erschbamer and Winkler, 1995; Molau, 1997; Erschbamer *et al.*, 1998; Diemer, 2002; Nicolè *et al.*, 2005; Weppler *et al.*, 2006). Such models are usually based on ramet dynamics but are nevertheless helpful because they allow us to overcome the difficulties of the long observation periods necessary to understand population processes in clonal plants (Watkinson and Powell, 1993). Demographic data of long-lived clonal plants at the genet level are still scarce (Menges, 2000), and very few studies have used matrix models and population viability analysis techniques to investigate genet longevity and population persistence. A notable exception is the work of Colling and Matthies (2006) on *Scorzonera humilis*, which revealed low mortality of adult genets and a life expectancy of several decades.

In a few cases, the transition probabilities between plant size stages or age stages in matrix models were used to estimate life span or population age distribution (Cochran and Ellner, 1992; Barot *et al.*, 2002). For *Silene acaulis*, for example, a size-based projection-matrix model revealed a life expectancy of more than 300 years for genets (Morris and Doak, 1998). Ehrlén and Lehtilä (2002) reviewed population matrix models for 71 herbaceous perennials and calculated species life spans ranging from 4 to approx. 1000 years, whereby more than half of the studied species had a life expectancy over 35 years. Their results agree reasonably well with previously published age estimates for long-lived plant species. However, most matrix models for clonal plants used in their study (86 %) were based on ramet data. It is important to recognize that understanding the life history of clonal plants should involve investigations at the genet level, too (Harper, 1977; Cook, 1985; de Steven, 1989; Eriksson, 1993; Fair *et al.*, 1999; Tanner, 2001; Araki *et al.*, 2009), although ramet dynamics may be used as an indirect measure of genet fitness, popualation growth and persistence (Caswell, 1985; Eriksson and Jerling, 1990; Weppler *et al.*, 2006). For example, Eriksson (1994) predicted that clonal populations of *Potentilla anserina*, *Rubus saxatilis* and *Linnaea borealis* consisting of more than 250 ramets are able to persist much longer then 50 years despite a negative population growth rate.

A challenge will be to employ demographic techniques on genet data obtained by molecular genotyping studies to make more accurate predictions at the genet level. For example, in a combined demographic–molecular approach to study growth patterns, reproduction and spatial expansion at the ramet level, it was possible to reveal spatio-temporal patterns at the genet level, and thus the characteristics particularly relevant to clonal life histories and population viability (Araki *et al.*, 2009; see also de Steven, 1989; Torimaru and Tomaru, 2005).

Somatic mutations and life span measurements

The use of genetic divergence generated by somatic mutations is a novel approach to measure genet size and to estimate life span (Heinze and Fussi, 2008). It is based on the fact that constant division of mitotic cells in clonal plants leads to the accumulation of somatic mutations over time (‘somatic mutation theory of clonality’, Klekowski, 1997). With this method, Gil *et al.* (2004; Table 1a) were able to date the origin of an *Ulmus procera* genet back to the time of the Romans, with some of its ramets growing as far apart as in Spain and Britain. The effective vegetative propagation and the deliberate plantation of this elm variety by humans explain the large distance between its ramets. In *Populus tremuloides*, molecular divergence detected by microsatellites was related to clone age with the help of demographic models of ramet and genet dynamics (Table 1a; Ally *et al.*, 2008). The resulting age estimates were up to 12 000 years, indicating that genet size of *Populus tremuloides* actually is not related to their life span. The formation of extra petals due to somatic mutations in buttercup (*Ranunculus repens*) was the key to establish a quick method to estimate the age of meadows by Warren (2009). Based on the frequency of this phenotypic change in buttercup of pastures of known age, he established a relationship between phenotypic change and meadow age. There is a similar link between increased frequency of pollen abortion and genet age for several clonal species (Harberd, 1967; Brighton *et al.*, 1983). However, thus far, somatic mutation rates have rarely been used for life span estimates, because somatic mutations cannot yet be detected efficiently (Gil *et al.*, 2004), and because somatic mutations are difficult to distinguish from allelic variation (Heinze and Fussi, 2008). Moreover, molecular divergence, due to somatic mutations, may differ between species (Klekowski and Godfrey, 1989), among populations (Gill *et al.*, 1995) and among genets (Schaal and Leverich, 1996), probably because somatic mutations may occur in response to environmental stress. In genets of *Pinus longaeva* ranging in age from 23 to 4713 years, no age-related accumulation of somatic mutations was detected at all (Lanner and Connor, 2001), while molecular divergence was found in distinct ramets of wild olive trees about 1000 years old (Baali-Cherif and Besnard, 2005). The incertitude concerning measured rates of somatic mutations remains a main concern for the precision of indirect life span estimates.

SENESCENCE AND AGEING IN CLONAL PLANTS

Clonal plants are considered to be immortal and several extreme life spans reported seem to confirm this. Senescence, defined here as the apparent weathering or a highly regulated deteriorative process (Leopold, 1975; see also Munné-Bosch, 2008), has indeed never been observed

in several plant species (e.g. *Rhododendron ferrugineum*, Escaravage *et al.*, 1998). Thus, genets do not reach their maximum age and eventually dying parts or ramets of clonal plants are constantly replaced by new ones (Watkinson and White, 1986). Senescence is not a necessary consequence of ageing with time in plants and there are many examples of death without senescence and of senescence without death (Thomas, 2002, 2003). Ecologically interpreted, a long life span is a compensation for erratic and hazardous seed production that is common in monocarpic plants (Molisch, 1938; Grime, 2001). Clearly, in clonal plants, fitness does not only rely on sexual but also on vegetative reproduction and is further enlarged by a long life span (Eriksson, 1988; Schmid, 1990; Fagerström, 1992). Clonal fitness is best defined as the 'rate of increase of a genet' (Fagerström *et al.*, 1998) and is maximized by the combination of three possible options of a meristem: (1) to propagate vegetatively, (2) to propagate sexually or (3) to remain dormant (Fagerström, 1992). Indeed, Tanner (2001) found a positive correlation between the expected remaining life span and genet size in clonal plants. Additionally, selection can act on eventual genetic variability among the modules of a genet resulting from somatic mutations (Antolin and Strobeck, 1985; Gill *et al.*, 1995; Fagerström *et al.*, 1998; Lushai and Loxdale, 2002). At least in theory, somatic mutations could give plants the ability to adapt to changing conditions throughout their lifetime (Salomonson, 1996; Pineda-Krch and Fagerström, 1999) and could thereby positively affect longevity of clonal plants (Breese *et al.*, 1965; Breese and Hayward, 1972; Klekowski, 1997).

On the other hand, genetic deterioration is sometimes assumed to cause senescence in long-lived plants (Thomas *et al.*, 2000). In his 'somatic mutation theory of clonality', Klekowski (1997, 2003) proposed that sexual reproductive success is inversely proportional to longevity, because the increasing age of a genet will make the accumulation of deleterious somatic mutations more likely. The accumulation rate of genetic load by somatic mutations in genets is not known, but infertility caused by mutations at one or only a few loci has been found, for example, in *Decodon verticillatus* (Eckert *et al.*, 1999). Another genetic mechanism leading to such a 'sexual extinction' is a change in polyploidy (Stebbins, 1971), as seed production can covary strongly with ploidy level (see, for example, *Butomus umbellatus*, Eckert, 2002). Despite these examples, an inherent molecular process leading to the death of a genet has, so far, not yet been identified in long-lived clonal plants. The long time persistence of genets in natural clonal populations will largely depend on meristem demography (e.g. Watson and Casper, 1984).

LONGEVITY AND POPULATION PERSISTENCE OF CLONAL PLANTS

Among the many traits enhancing population persistence, longevity of genets is, by far, the most important (Weiher *et al.*, 1999). Even populations that have a negative population growth rate are able to persist for long time periods due to the slow turnover rates of genets. The low extinction probability of genets results in a high persistence of well-established populations, which is typical for most clonal plant species (Helm *et al.*, 2006). Eriksson (1996, 2000) assessed the causal relationship between long-lived remnant populations and their function within their ecosystem. He suggests that remnant populations increase community and ecosystem stability as well as ecosystem resilience. First, this is due to vegetative recruitment that can directly buffer environmental variation experienced by a clonal population. Second, community resilience is increased by the continuous maintenance of similar habitat conditions created by the populations themselves, by balanced nutrient cycling and by enhanced (re-)colonization after disturbances. This phenomenon of positive species interactions stabilizing communities is also known as facilitation, an important process in community organization (Bertness and Leonard, 1997; Bruno *et al.*, 2003).

Arctic and alpine permanent vegetation types, such as grasslands and dwarf-shrub heaths, have been found to be very stable communities that have not been affected by past and recent climate changes (Grabherr and Nagy, 2003). The main reason for this appears to be the longevity of the mainly vegetatively reproducing members of such communities, reinforcing the hypothesis that long-lived clonal plants can enhance community and ecosystem resilience, thereby slowing vegetational change as a consequence of global warming (Guisan and Thuiller, 2005). On the other hand, analysis of available observational data has also revealed range expansions for several clonal species towards higher altitudes or latitudes (Pauli *et al.*, 1996; Walther *et al.*, 2002). Plant responses to artificially applied climate change included increased flowering, increased senescence of old modules and altered internal resource ratios (Carlsson and Callaghan, 1994; Callaghan *et al.*, 1997; Grabherr *et al.*, 2000). The indirect consequences were an increased rate of genet turnover and an increase of youger age-classes, indicating changes in population dynamics and structure. But more empirical data on current changes and the potential buffering of environmental variation by clonal plants will be necessary to make safe predictions about the future fate of old clonal populations when climate change is accelerating. Moreover, there is a need for studies that investigate population demography and viability. There are many age estimates for single genets, but there is only limited information on the variability of genet size and age at the population level that can form a basis for studies on the dynamics and persistence of clonal plant populations (Pornon *et al.*, 2000; van Kleunen *et al.*, 2001; Erschbamer and Winkler, 2005; Scheepens *et al.*, 2007). Depending on competitors and the success of seedling recruitment in dense populations, genets within a clonal population can differ considerably in size or age.

The level of genetic diversity is another important issue for the population viability of clonal plants. High genetic diversity can enable adaptation to changing climates, which in turn increases the persistence of populations. Asymmetric competition among differently sized genets can result in self-thinning, diversity loss and, in extreme cases, a monoclonal stand (Harberd, 1962; 1967; Oinonen, 1967; Williams, 1975). However, because clonal plants grow horizontally rather than in height, competition among genets is often found to be symmetric and genet diversity is maintained (Soane and Watkinson, 1979; Hartnett and Bazzaz, 1985; Cain, 1990; de Kroon *et al.*,

1992; Hara, 1994; van Kleunen *et al.*, 2001). Low sexual recruitment has long been reported to be a common feature of clonal plant populations (Eriksson, 1989; Schmid, 1990), but their size and age structure seem to be strongly shaped by sexual recruitment patterns (Kudoh *et al.*, 1999; Weppler *et al.*, 2006; Stöcklin *et al.*, 2009). Molecular studies of clonal plants found on average similar high levels of genetic diversity in clonal populations as in other plant species, indicating that seed recruitment does at least occasionally occur (Nybom, 2004) and that low levels of seedling recruitment in clonal plants are compensated for by the longevity of genets. In several populations of *Rhododendron ferrugineum*, next to very large and old individuals of about 260–300 years, many small and probably young genets were found (see Table 1; Escaravage *et al.*, 1998; Pornon *et al.*, 2000). Repeated seedling recruitment was also detected in populations of *Ranunculus repens* (Soane and Watkinson, 1979), *Calystegia collina* (Wolf *et al.*, 2000), in the rare orchid species *Cypripedium calceolus* (Brzosko *et al.*, 2002; Table 1c) and in populations of *Uvularia perfoliata* (Kudoh *et al.*, 1999). Studies that combine the estimation of maximum age with an investigation of genet size and age structure and a demographic analysis of ramet growth and seedling recruitment will help us to better understand population persistence, and will allow inferences to be made about their fate.

CONCLUSIONS

Our knowledge of plant longevity remains limited, particularly for clonal species. Methods to measure clonal plant age are either not appropriate, laborious or have inherent uncertainties. However, life span estimates of genets achieved by indirect methods, demographic approaches and the use of somatic mutations have increased our empirical knowledge considerably and thereby understanding of the structural and demographic properties of clonal plant populations. Maximum age estimates range from a few to several thousands of years and are an indicator for the slowest possible genet turnover rate and for population persistence. New molecular tools, used to estimate age indirectly, allow the investigation of size and age structure of whole populations instead of single genets and also on larger scales. Plant size estimates based on molecular fingerprinting can be critically evaluated with statistical methods, improving their accuracy. Because this is less the case for estimates of annual growth increments over hundreds or even thousands of years, age estimates are generally less accurate than estimates of genet size. Nevertheless, together with information on demography at the ramet and genet level, molecular data on whole populations provide a better tool to evaluate species life history and population viability. Next to maximum longevity, genet size and age structure, demography and genet diversity will be important for predicting population persistence in clonal plants and their ability to enhance community stability and ecosystem resilience under global change.

ACKNOWLEDGEMENTS

We are grateful to K. Giano, J. F. Scheepens, G. Armbruster, C. Körner, H. Thomas and an anonymous referee for valuable comments on earlier drafts of the manuscript. This work was supported by the European Commission's FP6 ECOCHANGE project Challenges in assessing and forecasting biodiversity and ecosystem changes in Europe (FP6 2006 GOCE 036866).

LITERATURE CITED

Aarssen LW. 2008. Death without sex – the 'problem of the small' and selection for reproductive economy in flowering plants. *Evolutionary Ecology* **22**: 279–298.

Agakhanyantz OE, Lopatin IK. 1978. Main characteristics of the ecosystems of the Pamirs, USSR. *Arctic and Alpine Research* **10**: 397–407.

Ally D, Ritland K, Otto SP. 2008. Can genet size serve as a proxy for clone age? An exploration using microsatellite divergence in *Populus tremuloides*. *Molecular Ecology* **17**: 4897–4911.

Alonso SB, Alonso-Villaverde V, Santiago JL, Martinez MC. 2007. Characteristics of grapevine (*Vitis vinifera* L.) 'Albarino' clones resulting from two clonal selections. *Hortscience* **42**: 97–100.

Antolin MF, Strobeck C. 1985. The population-genetics of somatic mutation in plants. *American Naturalist* **126**: 52–62.

Araki K, Shimatani K, Ohara M. 2009. Dynamics of distribution and performance of ramets constructing genets: a demographic-genetic study in a clonal plant, *Convallaria keiskei*. *Annals of Botany* **104**: 71–79.

Arens P, Coops H, Jansen J, Vosman B. 1998. Molecular genetic analysis of black poplar (*Populus nigra* L.) along Dutch rivers. *Molecular Ecology* **7**: 11–18.

Arnaud-Haond S, Duarte CM, Alberto F, Serrao EA. 2007. Standardizing methods to address clonality in population studies. *Molecular Ecology* **16**: 5115–5139.

Baali-Cherif D, Besnard G. 2005. High genetic diversity and clonal growth in relict populations of *Olea europaea* subsp. *laperrinei* (Oleaceae) from Hoggar, Algeria. *Annals of Botany* **96**: 823–830.

Bärlocher A, Schütz M, Krüsi BO, Wildi O. 2000. Development of species richness in mono-dominant colonies of tor grass (*Brachypodium pinnatum*) – an indicator of the impact of grazing upon subalpine grassland? In: Schütz M, Krüsi O, Edwards PJ. eds. *Succession research in the Swiss National Park*. Liestal: Scientific Council of the Swiss National Park, Nat.-park-Forsch. Schweiz, 89–105.

Barot S, Gignoux J, Legendre S. 2002. Stage-classified matrix models and age estimates. *Oikos* **96**: 56–61.

Barsoum N, Muller E, Skot L. 2004. Variations in levels of clonality among *Populus nigra* L. stands of different ages. *Evolutionary Ecology* **18**: 601–624.

Bell JNB, Tallis JH. 1973. *Empetrum nigrum* L. *The Journal of Ecology* **61**: 289–305.

Bertness MD, Leonard GH. 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* **78**: 1976–1989.

Bliss LC. 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics* **2**: 405–438.

Bonin A, Ehrich D, Manel S. 2007. Statistical analysis of amplified fragment length polymorphism data: a toolbox for molecular ecologists and evolutionists. *Molecular Ecology* **16**: 3737–3758.

Bory S, Lubinsky P, Risterucci AM, *et al*. 2008. Patterns of introduction and diversification of *Vanilla planifolia* (Orchidaceae) in Reunion Island (Indian Ocean). *American Journal of Botany* **95**: 805–815.

Breese EL, Hayward MD. 1972. Genetic basis of present breeding methods in forage crops. *Euphytica* **21**: 324–336.

Breese EL, Hayward MD, Thomas AC. 1965. Somatic selection in perennial ryegrass. *Heredity* **20**: 367–379.

Brighton CA, Mathew B, Rudall P. 1983. A detailed study of *Crocus speciosus* and its ally *C. pulchellus* (Iridaceae). *Plant Systematics and Evolution* **142**: 187–206.

Brown PM. 1996. OLDLIST: a database of maximum tree ages. In: Dean JS, Meko DM, Swetnam TW. eds. *Tree rings, environment, and humanity. Radiocarbon 1996*. Tucson, AZ: Department of Geosciences, The University of Arizona, 727–731.

Brundu G, Lupi R, Zapelli I, *et al*. 2008.. The origin of clonal diversity and structure of *Populus alba* in Sardinia: evidence from nuclear and plastid microsatellite markers. *Annals of Botany* **102**: 997–1006.

Bruno JF, Stachowicz JJ, Bertness MD. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* **18**: 119–125.

Brzosko E, Wroblewska A, Ratkiewicz M. 2002. Spatial genetic structure and clonal diversity of island populations of lady's slipper (*Cypripedium calceolus*) from the Biebrza National Park (northeast Poland). *Molecular Ecology* **11**: 2499–2509.

Cain ML. 1990. Models of clonal growth in *Solidago altissima*. *Journal of Ecology* **78**: 27–46.

Callaghan TV. 1973. A comparison of the growth of tundra plant species at several widely separated sites. *Merlewood Research and Development Paper* **53**: 1–52.

Callaghan TV. 1976. Growth and population-dynamics of *Carex bigelowii* in an Alpine environment – strategies of growth and population-dynamics of Tundra plants. *Oikos* **27**: 402–413.

Callaghan TV. 1980. Age-related patterns of nutrient allocation in *Lycopodium annotinum* from Swedish Lapland – strategies of growth and population-dynamics of Tundra plants. *Oikos* **35**: 373–386.

Callaghan TV, Carlsson BA. 1997. Impacts of climate change on demographic processes and population dynamics in Arctic plants. In: Oechel WC, Callaghan TV, Gilmanov T, Holten JI, Maxwell B, Molau U, Sveinbjornsson B. eds. *Ecological studies, global change and Arctic terrestrial ecosystems*. New York: Springer, 129–152.

Callaghan TV, Jonasson S, Brooker RW. 1997. Arctic clonal plants and global change. In: De Kroon H, Van Groenendaal J. eds. *The ecology and evolution of clonal plants*. Leiden: Backhuys Publishers, 381–403.

Carlsson BA, Callaghan TV. 1994. Impact of climate change factors on the clonal sedge *Carex bigelowii*: implications for population growth and vegetative spread. *Ecography* **17**: 321–330.

Caswell H. 1985. Evolutionary demography of clonal reproduction. In: Jackson JBC, Buss LW, Cook RE. eds. *Population biology and evolution of clonal organisms*. New Haven, CT: Yale University Press, 187–224.

Cochran ME, Ellner S. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecological Monographs* **62**: 345–364.

Colangelo WI, Lamont BB, Jones AS, Ward DJ, Bombardieri S. 2002. The anatomy and chemistry of the colour bands of grasstree stems (*Xanthorrhoea preissii*) used for plant age and fire history determination. *Annals of Botany* **89**: 605–612.

Colling G, Matthies D. 2006. Effects of habitat deterioration on population dynamics and extinction risk of an endangered, long-lived perennial herb (*Scorzonera humilis*). *Journal of Ecology* **94**: 959–972.

Cook RE. 1985. Growth and development in clonal plant populations. In: Jackson JBC, Buss LW, Cook RE. eds. *Population biology and evolution of clonal organisms*. New Haven, CT: Yale University Press, 259–296.

van der Hulst RGM, Mes THM, Den Nijs JCM, Bachmann K. 2000. Amplified fragment length polymorphism (AFLP) markers reveal that population structure of triploid dandelions (*Taraxacum officinale*) exhibits both clonality and recombination. *Molecular Ecology* **9**: 1–8.

Diemer M. 2002. Population stasis in a high-elevation herbaceous plant under moderate climate warming. *Basic and Applied Ecology* **3**: 77–83.

Dietz H, Fattorini M. 2002. Comparative analysis of growth rings in perennial forbs grown in an Alpine restoration experiment. *Annals of Botany* **90**: 663–668.

Dietz H, Ullmann I. 1997. Age-determination of dicotyledonous herbaceous perennials by means of annual rings: exception or rule? *Annals of Botany* **80**: 377–379.

Dietz H, Ullmann I. 1998. Ecological application of 'herbchronology': comparative stand age structure analyses of the invasive plant *Bunias orientalis* L. *Annals of Botany* **82**: 471–480.

Dietz H, Schweingruber FH. 2002. Annual rings in native and introduced forbs of lower Michigan, USA. *Canadian Journal of Botany-Revue Canadienne De Botanique* **80**: 642–649.

Douhovnikoff V, Dodd RS. 2003. Intra-clonal variation and a similarity threshold for identification of clones: application to *Salix exigua* using AFLP molecular markers. *Theoretical and Applied Genetics* **106**: 1307–1315.

Eckert CG. 2002. The loss of sex in clonal plants. *Evolutionary Ecology* **15**: 501–520.

Eckert CG, Dorken ME, Mitchell SA. 1999. Loss of sex in clonal populations of a flowering plant, *Decodon verticillatus* (Lythraceae). *Evolution* **53**: 1079–1092.

Ehrlén J, Lehtilä K. 2002. How perennial are perennial plants? *Oikos* **98**: 308–322.

Eriksson O. 1988. Ramet behaviour and population growth in the clonal herb *Potentilla anserina*. *The Journal of Ecology* **76**: 522–536.

Eriksson O. 1989. Seedling dynamics and life histories in clonal plants. *Oikos* **55**: 231–238.

Eriksson O. 1993. Genet dynamics of the clonal plants *Rubus saxatilis*. *Journal of Ecology* **81**: 533–542.

Eriksson O. 1994. Stochastic population dynamics of clonal plants: numerical experiments with ramet and genet models. *Ecological Research* **9**: 257–268.

Eriksson O. 1996. Regional dynamics of plants: a review of evidence for remnant, source–sink and metapopulations. *Oikos* **77**: 248–258.

Eriksson O. 2000. Functional roles of remnant plant populations in communities and ecosystems. *Global Ecology and Biogeography* **9**: 443–449.

Eriksson O, Jerling L. 1990. Hierarchical selection and risk spreading in clonal plants. In: van Groenendael J, de Kroon H. eds. *Clonal growth in plants: regulation and function*. The Hague: SPB Academic Publishing, 79–94.

Erschbamer B. 1994. Population dynamics of *Carex curvula* ssp. *rosae* and *Carex curvula* ssp. *curvula*. *Phytocoenologia* **24**: 579–596.

Erschbamer B, Retter V. 2004. How long can glacier foreland species live? *Flora* **199**: 500–504.

Erschbamer B, Winkler E. 1995. Shoot and leaf demography of *Carex curvula* ssp *curvula* and *Carex curvula* ssp *rosae* in the central Alps. *Journal of Vegetation Science* **6**: 593–598.

Erschbamer B, Winkler E. 2005. Long-term population development and spatial pattern of *Carex curvula* subspecies. *Arctic Antarctic and Alpine Research* **37**: 189–196.

Erschbamer B, Buratti U, Winkler J. 1998. Long-term population dynamics of two *Carex curvula* species in the central Alps on native and alien soils. *Oecologia* **115**: 114–119.

Escaravage N, Questiau S, Pornon A, Doche B, Taberlet P. 1998. Clonal diversity in a *Rhododendron ferrugineum* L. (Ericaceae) population inferred from AFLP markers. *Molecular Ecology* **7**: 975–982.

Fagerström T. 1992. The meristem-meristem cycle as a basis for defining fitness in clonal plants. *Oikos* **63**: 449–453.

Fagerström T, Briscoe DA, Sunnucks P. 1998. Evolution of mitotic cell-lineages in multicellular organisms. *Trends in Ecology and Evolution* **13**: 117–120.

Fair J, Lauenroth WK, Coffin DP. 1999. Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals. *Journal of Ecology* **87**: 233–243.

Franco M, Silvertown J. 1996. Life history variation in plants: an exploration of the fast–slow continuum hypothesis. *Philosophical Transactions: Biological Sciences* **351**: 1341–1348.

García MB, Antor RJ. 1995. Age and size structure in populations of a long-lived dioecious geophyte – *Borderea pyrenaica* (Dioscoreaceae). *International Journal of Plant Sciences* **156**: 236–243.

García MB, Pico FX, Ehrlén J. 2008. Life span correlates with population dynamics in perennial herbaceous plants. *American Journal of Botany* **95**: 258–262.

Gatsuk LE, Smirnova OV, Vorontzova LI, Zaugolnova LB, Zhukova LA. 1980. Age states of plants of various growth forms: a review. *Journal of Ecology* **68**: 675–696.

Gil L, Fuentes-Utrilla P, Soto A, Cervera MT, Collada C. 2004. Phylogeography: English elm is a 2000-year-old Roman clone. *Nature* **431**: 1053.

Gill DE, Chao L, Perkins SL, Wolf JB. 1995. Genetic mosaicism in plants and clonal animals. *Annual Review of Ecology and Systematics* **26**: 423–444.

Grabherr G, Nagy L. 2003. Alpine vegetation dynamics and climate change: a synthesis of long-term studies and observations. In: Nagy L, Grabherr G, Körner C, Thompson DBA. eds. *Alpine diversity in Europe*. New York, Springer, 399–409.

Grabherr G, Gottfried M, Pauli H. 2000. GLORIA: A Global Observation Research Initiative in Alpine Environments. *Mountain Research and Development* **20**: 190–191.

Grime JP. 2001. *Plant strategies, vegetation processes and ecosystem properties.* Chichester: Wiley.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**: 993–1009.

Hara T. 1994. Growth and competition in clonal plants – persistence of shoot populations and species diversity. *Folia Geobotanica and Phytotaxonomica* **29**: 181–201.

Harberd DJ. 1961. Observations on population struture and longevity of *Festuca rubra* L. *New Phytologist* **60**: 184–206.

Harberd DJ. 1962. Some observations on natural clones in *Festuca ovina*. *New Phytologist* **61**: 85–100.
Harberd DJ. 1967. Observations on natural clones in *Holcus mollis*. *New Phytologist* **66**: 401–408.
Harper. 1977.. *Population biology of plants*. London: Academic Press.
Hartnett DC, Bazzaz FA. 1985. The genet and ramet population dynamics of *Solidago canadensis* in an abandoned field. *Journal of Ecology* **73**: 407–413.
Heinze B, Fussi B. 2008. Somatic mutations as a useful tool for studying clonal dynamics in trees. *Molecular Ecology* **17**: 4779–4481.
Helm A, Hansi I, Pärtel M. 2006. Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters* **9**: 72–77.
Herben T, Hara T. 1997. Competition and spatial dynamics of clonal plants. In: De Kroon H, Van Groenendaal J. eds. *The ecology and evolution of clonal plants*. Leiden: Backhuys Publishers, 331–357.
Hutchings MJ, Wijesinghe D. 1997. Patchy habitat, division of labor and growth dividends in clonal plants. *Trends in Ecology and Evolution* **12**: 390–394.
Hutchinson TC. 1968. *Teucrium scorodonia* L. *Journal of Ecology* **56**: 901–911.
Inghe O, Tamm CO. 1985. Survival and flowering of perennial herbs. IV. The behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943–1981. *Oikos* **45**: 400–420.
Jäger EJ, Johst A, Lorenz H. 1997. Wuchsform und Lebensgeschichte von *Dictamnus albus* L. (Rutaceae). *Hercynia* **30**: 217–226.
Johnson LC, Johnson J. 1978. Methuselah: fertile senior citizen. *American Forests* **84**: 29–31.
Jones MH, Bay C, Nordenhall U. 1997. Effects of experimental warming on arctic willows (*Salix* spp.): a comparison of responses from the Canadian High Arctic, Alaskan Arctic, and Swedish Subarctic. *Global Change Biology* **3**: 55–60.
Jónsdóttir IS, Augner M, Fagerström T, Persson H, Stenström A. 2000. Genet age in marginal populations of two clonal *Carex* species in the Siberian Arctic. *Ecography* **23**: 402–412.
Jónsson TH. 2004. Stature of sub-arctic birch in relation to growth rate, life-span and tree from. *Annals of Botany* **94**: 753–762.
Kawano S. 1985. Life history characteristics of temperate woodland plants in Japan. In: White J. ed. *The population structure of vegetation. Handbook of Vegetation Science 3*. Dordrecht: Kluwer, 515–549.
Kemperman JA, Barnes BV. 1976. Clone size in American aspens. *Canadian Journal of Botany* **54**: 2603–2607.
Kihlman AO. 1890. Pflanzenbiologische Studien aus Russisch-Lappland. *Acta Societatis pro Fauna et Flora Fennica* **6**: 1–263.
Klekowski EJ. 1997. Somatic mutation theory of clonality. In: De Kroon H, Van Groenendael J. eds. *The ecology and evolution of clonal plants*. Leiden: Backhuys Publishers, 227–241.
Klekowski EJ. 2003. Plant clonality, mutation, diplontic selection and mutational meltdown. *Biological Journal of the Linnean Society* **79**: 61–67.
Klekowski EJ, Godfrey PJ. 1989. Ageing and mutation in plants. *Nature* **340**: 389–391.
van Kleunen M, Fischer M, Schmid B. 2001. Effects of intraspecific competition on size variation and reproductive allocation in a clonal plant. *Oikos* **94**: 515–524.
Körner C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems*. Berlin: Springer-Verlag.
Kraus G. 1873. Über Alter und Wachstumsverhältnisse ostgrönländischer Holzgewächse. *Botanische Zeitung* **33**: 513–518.
de Kroon H, Hara T, Kwant R. 1992. Size hierarchies of shoots and clones in clonal herb monocultures: do clonal and nonclonal plants compete differently? *Oikos* **63**: 410–419.
Kudoh H, Shibaike H, Takasu H, Whigham DF, Kawano S. 1999. Genet structure and determinants of clonal structure in a temperate deciduous woodland herb *Uvularia perfoliata*. *Journal of Ecology* **87**: 244–257.
Kuen V, Erschbamer B. 2002. Comparative study between morphology and age of *Trifolium pallescens* in a glacier foreland of the Central Alps. *Flora – Morphology, Distribution, Functional Ecology of Plants* **197**: 379–384.
Kull T, Kull K. 1991. Preliminary results from a study of populations of *Cypripedium calceolus* in Estonia. In: Wells TCE, Willems JH. eds. *Population ecology of terrestrial orchids*. The Hague: SPB Academic Publishing, 69–76.
Kullman L. 2008. Early postglacial appearance of tree species in northern Scandinavia: review and perspective. *Quaternary Science Reviews* **27**: 2467–2472.
Kuss P, Rees M, Ægisdóttir HH, Ellner SP, Stöcklin J. 2008. Evolutionary demography of long-lived monocarpic perennials: a time-lagged integral projection model. *Journal of Ecology* **96**: 821–832
Laberge MJ, Payette S, Bousquet J. 2000. Lifespan and biomass allocation of stunted black spruce clones in the subarctic environment. *Journal of Ecology* **88**: 584–593.
Lanner RM, Connor KF. 2001. Does bristlecone pine senesce? *Experimental Gerontology* **36**: 675–685.
Lasso E. 2008. The importance of setting the right genetic distance threshold for identification of clones using amplified fragment length polymorphism: a case study with five species in the tropical plant genus *Piper*. *Molecular Ecology Resources* **8**: 74–82.
Legère A, Payette S. 1981. Ecology of a black spruce (*Picea mariana*) clonal population in the hemiarctic zone, northern Quebec – population-dynamics and spatial development. *Arctic and Alpine Research* **13**: 261–276.
Leopold AC. 1975. Aging, senescence, and turnover in plants. *BioScience* **25**: 659–662.
Lubinsky P, Bory S, Hernandez J, Kim SC, Gomez–Pompa A. 2008. Origins and dispersal of cultivated vanilla (*Vanilla planifolia* Jacks. [Orchidaceae]). *Economic Botany* **62**: 127–138.
Lushai G, Loxdale HD. 2002. The biological improbability of a clone. *Genetical Research* **79**: 1–9.
Lynch A, Barnes JJRW, Cambecedes J, Vaillancourt RE. 1998. Genetic evidence that *Lomatia tasmanica* (Proteaceae) is an ancient clone. *Australian Journal of Botany* **46**: 25–33.
McCarthy DP. 1992. Dating with cushion plants: establishment of a *Silene acaulis* growth curve in the Canadian Rockies. *Arctic, Antarctic and Alpine Research* **24**: 50–55.
Menges ES. 2000. Population viability analyses in plants: challenges and opportunities. *Trends in Ecology & Evolution* **15**: 51–56.
Mock KE, Rowe CA, Hooten MB, Dewoody J, Hipkins VD. 2008. Clonal dynamics in western North American aspen (*Populus tremuloides*). *Molecular Ecology* **17**: 4827–4844.
Molau U. 1997. Age-related growth and reproduction in *Diapensia lapponica*, an arctic–alpine cushion plant. *Nordic Journal of Botany* **17**: 225–234.
Molisch H. 1929. *Die Lebensdauer der Pflanze*. Jena: Gustav Fischer.
Molisch H. 1938. *The longevity of plants*. Lancaster: Science Press.
Mork E. 1946. Om skogsbunnens lyngvegetasjon. *Meddelser fra det Norske Skogforsoksvesen* **33**: 274–356.
Morris WF, Doak DF. 1998. Life history of the long-lived gynodioecious cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices. *American Journal of Botany* **85**: 784–793.
Morris WF, Pfister CA, Tuljapurkar S. 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* **89**: 19–25.
Mueller UG, Wolfenbarger LL. 1999. AFLP genotyping and fingerprinting. *Trends in Ecology and Evolution* **14**: 389–394.
Munné-Bosch S. 2008. Do perennials really senesce? *Trends in Plant Science* **13**: 216–220.
Nicolè FE, Brzosko E, Till-Bottraud I. 2005. Population viability analysis of *Cypripedium calceolus* in a protected area: longevity, stability and persistence. *Journal of Ecology* **93**: 716–726.
Nybom H. 2004. Comparison of different nuclear DNA markers for estimating intraspecific genetic diversity in plants. *Molecular Ecology* **13**: 1143–1155.
Oinonen E. 1967. The correlation between the size of Finnish bracken (*Pteridium aquilinum* (L.) Kuhn) clones and certain periods of site history. *Acta Forestalia Fennica* **7**: 1–51.
Oinonen E. 1969. The time table of vegetative spreading of the lily-of-the-valley *Convallaria majalis* L. and the wood small-reed *Calamagrostis epigeios* (L.) Roth in southern Finland. *Acta Forestalia Fennica* **97**: 1–35.
Parks JC, Werth CR. 1993. A study of spatial features of xlones in a population of bracken fern, *Pteridium aquilinum* (Dennstaedtiaceae). *American Journal of Botany* **80**: 537–544.
Pauli H, Gottfried M, Grabherr G. 1996. Effects of climate change on mountain ecosystems – upward shifting of alpine plants. *World Resource Review* **8**: 382–390.

Perkins DL, Parks CG. 2006. Age structure and age-related performance of sulfur cinquefoil (*Potentilla recta*). *Weed Science* **54**: 87–93.

Pineda-Krch M, Fagerström T. 1999. On the potential for evolutionary change in meristematic cell lineages through intraorganismal selection. *Journal of Evolutionary Biology* **12**: 681–688.

Pompanon F, Bonin A, Bellemain E, Taberlet P. 2005. Genotyping errors: causes, consequences and solutions. *Nature Reviews Genetics* **6**: 847–859.

Pornon A, Escaravage N, Till-Bottraud I, Doche B. 1997. Variation of reproductive traits in *Rhododendron ferrugineum* L. (Ericaceae) populations along a successional gradient. *Plant Ecology* **130**: 1–11.

Pornon A, Escaravage N, Thomas P, Taberlet P. 2000. Dynamics of genotypic structure in clonal *Rhododendron ferrugineum* (Ericaceae) populations. *Molecular Ecology* **9**: 1099–1111.

Poschlod P, Matthies D, Jordan S, Mengel C. 1996. The biological flora of Central Europe. An ecological bibliography. *Bulletin of the Geobotanical Institute ETH* **62**: 89–108.

Rabotnov TA. 1950. The life cycle of perennial herbaceous plants in meadow coenoses (in Russian). *Proceedings of the Botanical Institute of Academy of Sciences of USSR* **6**: 7–197.

Reusch TBH, Stam WT, Olsen JL. 1998. Size and estimated age of genets in eelgrass, *Zostera marina*, assessed with microsatellite markers. *Marine Biology* **133**: 519–525.

Rixen C, Casteller A, Schweingruber FH, Stoeckli V. 2004. Age analysis helps to estimate plant performance on ski pistes. *Botanica Helvetica* **114**: 127–138.

Salomonson A. 1996. Interactions between somatic mutations and plant development. *Vegetatio* **127**: 71–75.

Schaal BA, Leverich WJ. 1996. Molecular variation in isolated plant populations. *Plant Species Biology* **11**: 33–40.

Scheepens JF, Veeneklaas RM, Van de Zande L, Bakker JP. 2007. Clonal structure of *Elytrigia atherica* along different successional stages of a salt marsh. *Molecular Ecology* **16**: 1115–1124.

Schmid B. 1990. Some ecological and evolutionary consequences of modular organization and clonal growth in plants. *Evolutionary Trends in Plants* **4**: 25–34.

Schulman E. 1958. Bristlecone pine, oldest known living thing. *National Geographic* **113**: 355–372.

Schweingruber FH, Dietz H. 2001. Annual rings in the xylem of dwarf shrubs and perennial dicotyledonous herbs. *Dendrochronologia* **19**: 115–126.

Schweingruber F, Poschlod P. 2005. Growth rings in herbs and shrubs: life-span, age determination and stem anatomy. *Forest Snow and Landscape Research* **79**: 195–415.

Sharitz RR, McCormick JF. 1973. Population dynamics of two competing annual plant species. *Ecology* **54**: 723–740.

Shirreffs DA. 1985. *Anemone nemorosa* L. *Journal of Ecology* **73**: 1005–1020.

Silvertown J. 1991. Modularity, reproductive thresholds and plant population dynamics. *Functional Ecology* **5**: 577–580.

Silvertown J, Lovett Doust L. 1993. *Introduction to plant population biology*. London: Blackwell Scientific Publications.

Silvertown J, Franco M, Pisanty I, Mendoza A. 1993. Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* **81**: 465–476.

Soane ID, Watkinson AR. 1979. Clonal variation in populations of *Ranunculus repens*. *New Phytologist* **82**: 557–573.

Stebbins GL. 1971. *Chromosomal evolution in higher plants*. London: Edward Arnold.

Stehlik I, Holderegger R. 2000. Spatial genetic structure and clonal diversity of *Anemone nemorosa* in late successional deciduous woodlands of Central Europe. *Journal of Ecology* **88**: 424–435.

Steinger T, Körner C, Schmid B. 1996. Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula*. *Oecologia* **105**: 94–99.

de Steven D. 1989. Genet and ramet demography of *Oenocarpus mapora* ssp. *mapora*, a clonal palm of Panamanian tropical moist forest. *Journal of Ecology* **77**: 579–596.

Stöcklin J. 1992. Environment, morphology and growth of clonal plants, an overview. *Botanica Helvetica* **102**: 3–21.

Stöcklin J, Kuss P, Pluess AR. 2009. Genetic diversity, phenotypic variation and local adaptation in the alpine landscape: case studies with alpine plant species. *Botanica Helvetica* **119**: 125–133.

Suvanto LI, Latva-Karjanmaa TB. 2005. Clone identification and clonal structure of the European aspen (*Populus tremula*). *Molecular Ecology* **14**: 2851–2860.

Suyama Y, Obayashi K, Hayashi I. 2000. Clonal structure in a dwarf bamboo (*Sasa senanensis*) population inferred from amplified fragment length polymorphism (AFLP) fingerprints. *Molecular Ecology* **9**: 901–906.

Tamm CO. 1948. Observations on reproduction and survival of some perennial herbs. *Botaniska Notiser* **3**: 305–321.

Tamm CO. 1956. Further observations on the survival and flowering of some perennial herbs. *Oikos* **7**: 274–292.

Tanner JE. 2001. The influence of clonality on demography: patterns in expected longevity and survivorship. *Ecology* **82**: 1971–1981.

Thomas H. 2002. Ageing in plants. *Mechanisms of Ageing and Development* **123**: 747–753.

Thomas H. 2003. Do green plants age, and if so, how? In: Nyström T, Osiewacz HD. eds. *Topics in current genetics*. New York: Springer, 145–171.

Thomas H, Thomas HM, Ougham H. 2000. Annuality, perenniality and cell death. *Journal of Experimental Botany* **51**: 1781–1788.

Torimaru T, Tomaru N. 2005. Fine-scale clonal structure and diversity within patches of a clone-forming dioecious shrub, *Ilex leucoclada* (Aquifoliaceae). *Annals of Botany* **95**: 295–304.

Troll W. 1937. *Vergleichende Morphologie der höheren Pflanzen*. Berlin: Bornträger.

Vasek FC. 1980. Creosote bush – long-lived clones in the Mojave desert. *American Journal of Botany* **67**: 246–255.

Von Arx G, Dietz H. 2005. Automated image analysis of annual rings in the roots of perennial forbs. *International Journal of Plant Sciences* **166**: 723–732.

Vorontzova LI, Zaugolnova LB. 1985. Population biology of Steppe plants. In: White J. ed. *The population structure of vegetation. Handbook of vegetation science*. Dordrecht: Kluwer, 143–178.

Vouillamoz JD, Maigre D, Meredith CP. 2003. Microsatellite analysis of ancient alpine grape cultivars: pedigree reconstruction of *Vitis vinifera* L. 'Cornalin du Valais'. *Theoretical and Applied Genetics* **107**: 448–454.

Walther GR, Post E, Convey P, *et al.* 2002. Ecological responses to recent climate change. *Nature* **416**: 389–395.

Ward DJ, Lamont BB, Burrows CL. 2001. Grasstrees reveal contrasting fire regimes in eucalypt forest before and after European settlement of southwestern Australia. *Forest Ecology and Management* **150**: 323–329.

Warren J. 2009. Extra petals in the buttercup (*Ranunculus repens*) provide a quick method to estimate the age of meadows. *Annals of Botany* **104**: 785–788.

Watkinson AR, Powell JC. 1993. Seedling recruitment and the maintenance of clonal diversity in plant-populations – a computer-simulation of *Ranunculus repens*. *Journal of Ecology* **81**: 707–717.

Watkinson AR, White J. 1986. Some life-history consequences of modular construction in plants. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* **313**: 31–51.

Watson MA, Casper BB. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. *Annual Review of Ecology and Systematics* **15**: 233–258.

Weiher EA, Van der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* **10**: 609–620.

Weppler T, Stoll P, Stöcklin J. 2006. The relative importance of sexual and clonal reproduction for population growth in the long-lived alpine plant *Geum reptans*. *Journal of Ecology* **94**: 869–879.

Wesche K, Ronnenberg K, Hensen I. 2005. Lack of sexual reproduction within mountain steppe populations of the clonal shrub *Juniperus sabina* L. in semi-arid southern Mongolia. *Journal of Arid Environments* **63**: 390–405.

Wherry ET. 1972. Box-huckleberry as the oldest living protoplasm. *Castanea* **37**: 94–95.

Widen BN, Cronberg N, Widen M. 1994. Genotypic diversity, molecular markers and spatial-distribution of genets in clonal plants, a literature survey. *Folia Geobotanica and Phytotaxonomica* **29**: 245–263.

Williams GC. 1975. *Sex and evolution.* Princeton, NJ: Princeton University Press.

Wittig R, Jungmann R, Ballach HJ. 2007. The extent of clonality in large stands of *Lycopodium annotinum* L. *Flora* **202**: 98–105.

Wolf AT, Howe RW, Hamrick JL. 2000. Genetic diversity and population structure of the serpentine endemic *Calystegia collina* (Convolvulaceae) in northern California. *American Journal of Botany* **87**: 1138–1146.

Zoller H. 1949. Beitrag zur Alterbestimmung von Pflanzen aus der Walliser Felsensteppe. *Berichte über das Geobotanische Forschungsinstitut Rübel in Zürich für das Jahr* **1948**: 61–68.