

REVIEW

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

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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)	
<i>Olea europaea</i> subsp. <i>laperrinei</i>	Molecular markers	80 m ² +	1000 +	–	Baali-Cherif and Besnard (2005)	
<i>Picea abies</i>	Radiocarbon dating	–	10 000 – 12 000	–	Kullman (2008)	
<i>Picea mariana</i>	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 <i>et al.</i> (2000)	
<i>Pinus longaeva</i>	Growth ring analysis	–	4900	–	Schulman (1958), Johnson and Johnson (1978), Brown (1996)	
<i>Populus alba</i>	Molecular markers	–	> 12 000	–	Brundu <i>et al.</i> (2008)	
<i>Populus tremuloides</i>	Morphological analysis, aerial photographs	510	10 000 +	–	Kemperman and Barnes (1976)	
	Microsatellite divergence based on mutation accumulation	–	12 000	14	Ally <i>et al.</i> (2008)	
<i>Populus tremula</i>	Molecular markers	16	152	2	Suvanto and Latva-Karjanmaa (2005)	
<i>Ulmus procera</i>	Molecular markers and microsatellite divergence based on mutation accumulation	–	2000	–	Gil <i>et al.</i> (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)
<i>Arctostaphylos alpina</i>	Growth ring analysis	–	–	93	–	Schweingruber and Poschlod (2005)
<i>Calluna vulgaris</i>	Growth ring analysis	–	–	58	–	Mork (1946)
<i>Dryas octopetala</i>	Growth ring analysis	–	–	108	–	Kihlman (1890)
<i>Empetrum nigrum</i> ssp. <i>nigrum</i>	Growth ring analysis	–	–	140	–	Bell and Tallis (1973)
<i>Erica carnea</i>	Growth ring analysis	–	–	82	–	Schweingruber and Poschlod (2005)
<i>Juniperus sabina</i>	Growth ring analysis	–	–	67–70	–	Molisch (1929)
	Molecular markers	795 m ²	1.8–6.8	770–2940	–	Wesche <i>et al.</i> (2005)
<i>Larrea tridentata</i>	Molecular markers, growth rings, radiocarbon dating	16.6	–	11 700	–	Vasek (1980)
	Growth rings, radiocarbon dating	11	–	9170	–	Vasek (1980)
<i>Loiseleuria procumbens</i>	Growth ring analysis	–	–	110	–	Schweingruber and Poschlod (2005)
<i>Lomatia tasmanica</i>	Molecular markers, chromosome counts and radiocarbon dating	1200	–	43 600	–	Lynch <i>et al.</i> (1998)
<i>Rhododendron ferrugineum</i>	Growth ring analysis	–	–	202	–	Schweingruber and Poschlod (2005)
	Molecular markers	20 m ²	2.6	300	–	Escaravage <i>et al.</i> (1998)
	Molecular markers	25 m ²	115	283 +	28	Pornon <i>et al.</i> (2000)
<i>Salix arctica</i>	Growth ring analysis	–	–	150	–	Kraus (1873)
<i>Vaccinium vitis-idaea</i>	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
<i>Acantholimon diapensoides</i>	?	–	–	400	Agakhanyantz and Lopatin (1978)
<i>Anemone nemorosa</i>	Growth ring analysis	–	–	>5	Shirreffs (1985)
	Molecular markers	12	1.9–3.1	190–320	Stehlik and Holderegger (2000)
<i>Calamagrostis epigejos</i>	Comparative analysis of site history and genet size	50	–	400	Oinonen (1969)
<i>Convallaria majalis</i>	Comparative analysis of site history and genet size	850	–	670 +	Oinonen (1969)
<i>Cypripedium calceolus</i>	Molecular markers	39 ramets	1–1.5	370	Brzosko <i>et al.</i> (2002)
<i>Gaylussacia brachycerium</i>	Morphological analysis	1980	–	13 000 +	Wherry (1972)
<i>Silene acaulis</i>	Growth ring analysis	–	–	252	McCarthy (1992)
	Modelling: size-based population projection matrices	>0.2	–	300 +	Morris and Doak (1998)
<i>Teucrium scorodonia</i>	Morphological analysis	Several square metres	–	50–100	Hutchinson (1968)
<i>Trifolium alpinum</i>	Growth ring analysis	–	–	50	Schweingruber and Poschold (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
<i>Calamagrostis epigejos</i>	Comparative analysis of site history and genet size	50	–	400 +	Oinonen (1969)
<i>Carex curvula</i>	Molecular markers	1.6	0.04	2000	Steinger <i>et al.</i> (1996)
<i>Carex ensifolia</i> ssp. <i>arctisibirica</i>	Molecular markers	40	–	3800 +	Jónsdóttir <i>et al.</i> (2000)
<i>Carex stans</i>	Molecular markers	7.4	–	Approx. 150	Jónsdóttir <i>et al.</i> (2000)
<i>Festuca ovina</i>	Morphological analysis, cross-pollination tests	8.25	0.3	1000 +	Harberd (1962)
<i>Festuca rubra</i>	Morphological analysis, cross-pollination tests	220	22.9	1000 +	Harberd (1961)
<i>Holcus mollis</i>	Morphological and phenological analysis, chromosome analysis	880	–	1000 +	Harberd (1967)
<i>Sasa senanensis</i>	Molecular markers	300	Approx. 100	Several decades	Suyama <i>et al.</i> (2000)
<i>Stipa pennata</i>	Calendar age determination (Gatsuk <i>et al.</i> , 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
<i>Lycopodium annotinum</i>	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 <i>et al.</i> (2007)
<i>Lycopodium comoplanatum</i>	Comparative analysis of site history and genet size	250	–	850	Oinonen (1969)
<i>Peridium aquilinum</i>	Comparative analysis of site history and genet size	489	–	1400	Oinonen (1967)
<i>Zostera marina</i>	Molecular markers	1015	43	1180	Parks and Werth (1993)
	Molecular markers	33	13	134	Reusch <i>et al.</i> (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 grasses 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 Zaigolnova, 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 assignment 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; Wepler *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, population growth and persistence (Caswell, 1985; Eriksson and Jerling, 1990; Wepler *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 than 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 uncertainty 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 younger 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; Wepler *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; Pomon *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).

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