REVIEW PAPER

Prerequisites for the Reproduction of Wild Cherry (*Prunus avium* L.)

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Abstract

Owing to its considerable capacity of seed dispersal and rapid propagation through adventitious sprouts from the root system, Wild cherry (*Prunus avium* L.) behaves as a colonizing species of initial succession stages and during progressing succession of the local disturbance it may become a component of climax or close-to-climax mesophilous forest ecosystems. A policy of non-management, especially following winter storms, may help maintain genetic diversity of Wild cherry through increased levels of both sexual and clonal recruitment. The aim of this review is an overview on the state of the knowledge about management influences on reproductive strategy of Wild cherry within the scope of its phenological behaviour. The vegetative and generative phenological behaviour of Wild cherry occurring as the result of ontogenetic variations in the traits of the trees and their parts could be monitored and described and the role of management (or environment) influences in determining this behaviour could be related. Some of the hypotheses, which are to be discussed in the research of Wild cherry reproduction, are presented in detail.

Key words: management influences, phenological behaviour, Prunus avium, reproduction

Introduction

A management strategy for a particular species must be based on the available knowledge about the biology of that species and on the basic theories regarding ecology and genetics. Giving an overview on the state of the knowledge about management influences on reproductive strategy of Wild cherry within the scope of its phenological behaviour seems to be an appropriate motivation for this review. The material used in this review comprises articles extracted from the literature as well as web-reports and other free web-records focused on the woody angiosperms of temperate and boreal zones and related to the various aspects of regeneration and reiteration of Wild cherry. The literature overview is presented referring to the species' characteristics, management and reproduction considerations.

Wild cherry

Open-branched deciduous tree up to 23(35) m tall with a trunk up to 1.5 m diameter, producing no root-stock, attaining an age of up to 200 years (Chukhina

2008). It is not a long-lived tree and generally begins to decay before reaching 100 years (Elwes and Henry 1913). Young trees show strong apical dominance with a straight trunk and symmetrical conical crown, becoming rounded to irregular on old trees. Bark is smooth, reddish or purple-brown in color with a metallic copper sheen, with prominent horizontal grey-brown lenticels or breathing pores in bands around the trunk, often peeling off on the surface in transverse annular strips, becoming thick dark blackish-brown and deeply fissured at the base of old trunks. Young branchlets glabrous, gray-brown, buds reddish brown. Crown shoots are characterised by vigorous 'long-shoots' (Dick and Leakey 2006), which form the main structure of the crown (branches) and 'short-shoots' which are very slow-growing lateral spurs, with very short internodes (1–2 mm) which carry most of the leaves of the crown. Flowers are initiated in the axils of these short-shoot leaves and develop as clusters of fruits (reproductive spurs). Leaves alternate on the long shoots, clustered at the apices of the short shoots or spurs, variable in shape and size, up to 16 cm long and 8 cm wide (up to 5 in. long and 2 in. broad: Elwes and Henry 1913), ovate

or obovate, elliptic or oblong, cuspidate-acuminate at the apex, cuneate or rounded at the base, biserrate or unequally serrate, the serrations tipped with a gland; upper surface dull, glabrescent; lower surface pale green, with persistent appressed hairs, mainly on the midrib and nerves; lateral nerves, twelve to sixteen pairs, looping before reaching the margin; petiole with a few scattered hairs, and usually with a pair of red prominent glands near its distal end; stipules are linear, adenodentate. In autumn leaves turn a mosaic of vivid reds and yellows, orange, crimson, and purple before falling. Inflorescences have no leaves at the base. Flowers are hermaphroditic, appearing with the leaves, two to six in a cluster, set on naked pedicels 2.5–6 cm long, and usually situated on the spur shoots, arising out of a bud, with no internal leafy scales; calyx-tube constricted near the apex, glabrous, with five entire reflexed lobes: petals pure white, obovate-rounded, emarginate; sepals are obtuse, usually smooth-edged, deflected; stamens 35 or 36. In the pistil, there are regularly two ovules but only one grows to seed. Fruits of wild plants are about 1 cm in diameter, globose, smooth, shining, ranging in colour from dark red to dark purple (often referred to as "black") when mature in mid summer, having for the most part a bitter or, quite infrequently, sweet flavour, with juicy pulp. "In the wild and typical form of the species, the fruit is small, with little edible flesh" (Elwes and Henry 1913). Stones are smooth, light brown, oval, compressed, furrowed on one edge. All parts of the plant (e.g., leaves, bark, and seeds) except for the ripe fruit are slightly toxic, containing hydrogen cyanide (as is indicated by that bark's "bitter almond" scent or taste; Mitchell 1994, Rushforth 1999). In small quantities, hydrogen cyanide has been shown to stimulate respiration and improve digestion, it is also claimed to be of benefit in the treatment of cancer. *P. avium* is diploid (2n = 16, sometimes 17, 18).

This species suckers if the roots are damaged (Fern 1997), layers, and when cut down, coppices. Root suckers often develop around mature trees and eventually grow as large as the parents, forming clumps or small woodlands. Natural regeneration of Wild cherry in the forests of West Ukraine from seed, coppice, and root suckers was found to occur freely, the root suckers accounting for 71% of the total (Mjakusko 1964). In France, Wild cherry is a tree species characterised either by scattered isolated single trees, or groups of trees, or trees in well established stands (Bellefontaine et al. 2003). In the latter case the stands can be "normal", in which the cherry represent more than 20% of the stems regularly distributed in an area of more than 0.5 ha, or

the stands can be described as border line, where over a length of 10 to 50 m, cherry represent more than 10% of the stems. In the case of groups (clump stands), the greatest distance between two trees of the same genotype is 81 metres (Fernandez et al. 1994). The maximum suckering clump (clonal group) size recorded by Vaughan et al. (2007) exceeded 800 m².

Prunus avium was named by Linneaus in 1755 (Faust and Surányi 1997). It is commonly called the Wild cherry, Sweet cherry, Mazzard, and Gean (Elwes and Henry 1913). Beaver et al. (1995) suggested that *P. fruticosa, P. cerasus* and *P. avium* share a common gene pool and/or are continually sharing alleles through introgression. Hedrick (1915) described the geographic range of *P. avium* as all of mainland Europe well into the southern U.S.S.R. and as far east as northern India, with the greatest prevalence between the Caspian sea and the Black sea – in the region of the Caucasus Mountains, where is located its maximum diversity (Terekhina 2008). Wild cherry is widely distributed throughout nearly the whole of Europe, but appears to be rare in Spain and Italy as a wild tree (Elwes and Henry 1913). Its natural range covers the temperate regions of Europe, from northern Spain to the south eastern Russia (Hedrick 1915); also found throughout the British Isles except northern Scotland. It extends as far north as the province of Bergen in Norway (Elwes and Henry 1913).

Nowadays Wild cherry is used extensively in Europe for the afforestation of agricultural land and it is also valued for wildlife and amenity plantings, wood production in natural forests and in plantations (Zimmermann 1988, Schalk 1990). It has been utilized to breed cherry cultivars with resistance to frost and a number of diseases (Tydeman et al. 1966, Tobutt 1985, Nicoll 1993, Chukhina 2008). The following varieties of P. avium, cultivated for ornament, are peculiar in leaves, flowers, or habit (Elwes and Henry 1913): var. decumana Koch (1869) – leaves very large, occasionally as much as 10 to 12 in. in length, and 4 to 6 in. in breadth; var. *asplenifolia* Kirchn. (1864) – leaves with deeply incised teeth; var. *salicifolia* Dipp. (1893) – leaves very narrow; var. *plena* Hort. (Hort, means common usage by horticulturists) – flowers partially or completely double; var. *pyramidalis* Hort. – pyramidal crown; var. *pendula* Hort. – drooping crown. This species is a parent of many sweet cherry cultivars (Fern 1997, Porcher Michel et al. 2004; Table 1).

Management considerations

Early and abundant flowering is induced by adequate pruning, tearing and bending of branches, weed control and root pruning (de Cuyper 2008).

Table 1. Typical *Prunus avium* (L.) L. cultivars. From Porcher Michel H. et al. (2004), Tobutt et al. (2005)

Group (Synonym)	Cultivars (Synonym)	Incompatibility group, allele pair
Mazzards – the fruit is small and varies in shape and color.	English mazzard 'Charger'	O, S_1S_7
	Belgium (German) mazzard	No information
	'Limburger Vogelkirsche'	No information
	American mazzard 'Saylor'	
Geans (Hearts) - the fruit is heart-shaped and has a soft flesh.	'Black Tartarian'	I, S_1S_2
	'Governor Wood'	VI, S_3S_6
	'Roundel'	I, S_1S_2
Bigarreaus – the fruit is heart-shaped and with hard flesh.	'Große Schwarze Knorpel' ('Large Black Bigarreau')	No information
		XVI, S_3S_9
	'Moreau' ('Bigarreau Moreau')	III, S_3S_4
	'Napoleon' ('Lauerman', 'Royal Ann')	II, S_1S_3
		III, S_3S_4
	'Windsor'	
	'Yellow Spanish'	

Flowering starts from about 4 years of age at dbh 4 cm under optimal conditions. Wild cherry is entomophilous, with bumblebees and hoverflies (*Bombus* spp. and *Rhingia* spp.) acting as main pollen vectors. Bumble bees display a particular foraging behaviour, which leads one to suspect a small-scaled patch-like pollination pattern within Wild cherry populations (Heinrich 1976, Goulson et al. 1998). Although flowering takes place every year, it is not always followed by a seed crop (Suszka et al. 1996). Indeed, late frosts can destroy the flowers and rain or cold can prevent bees from collecting and transporting pollen. Fertilization occurrs six days after pollination (Hedhly et al. 2007). The effective pollination period is conditioned by three main processes – stigmatic receptivity, pollen tube kinetics and ovule development (Sanzol and Herrero 2001). Wild cherries start producing significant quantities of fruits from the age of 15 years; fruiting has even been seen sometimes from the age of 6 to 7 years. Traditional pomological techniques are applied to increase fruit production, such as planting in espalier, use of bird nets and placing of several bumble bee nests (de Cuyper 2008). Late-maturing cherries (80 days between flowering and maturity) produce 100% of healthy and well developed seeds capable of germinating (Suszka et al. 1996). An intermediate seed formation is found in varieties requiring 60 to 75 days for fruit maturation. Concentration of total soluble solids and flavour are the best standards for judging the optimum time of harvesting (Jindal et al. 2008).

Wild cherries attract many insects. Wasps strip the flesh from the fruit and leave the stones hanging suspended in bunches. The fruit are readily eaten by numerous birds, especially pigeons, thrushes, starlings and jays, and by small mammals like foxes, which digest the fruit flesh and disperse the seeds in their droppings. Some rodents, and a few birds (notably the hawfinch), also crack open the stones to eat the ker-

nel inside. The stones can survive and germinate in the first, second and even third spring. It has been found (Suszka et al. 1996) that a rapid elevation of temperature in the spring acts as an inducer of dormancy, dividing the population of buried seeds into subpopulations capable of germinating in different years. If sown immediately after collection, the seeds of Wild cherry are not dormant, but become so if stored (Zachej 1958). "The seed, if put in a rot-heap when ripe, will germinate the following spring, though when kept dry for long, a large proportion will lie dormant for a year before coming up" (Elwes and Henry 1913). A negative relationship that appeared between seed size and germination for Wild cherry was reported by Esen et al. (2006); high variation in seed soundness was reported by Tukey (1927), Grisez (1974), and Esen et al. (2006). 'Tree-to-tree variation' and variation within the same tree of Wild cherry or seed polymorphism might act as significant determinants for variable germination behaviors among seed-sources (Grisez 1974, Radosevich et al. 1997, Finch-Savage 2001, Finch-Savage et al. 2002, Esen et al. 2006).

Typical of pioneer tree species such as Wild cherry is that they colonize early forest successsional stages as a result of forest disturbances – larger gaps in the forest canopy (Höltken and Gregorius 2007). Wild cherry is a species without advance regeneration and implies that seedlings cannot be established under a closed canopy and they can be established and/or grow only in gaps (after Yamamoto 2000). Such gaps (up to 60 m in diameter) are, for example, provided in shelterwood forests, where a group selection method of cutting is applied. Wild cherry seedlings easily germinate under a canopy (Pryor 1988); however, the seedlings die off if they are not exposed to a lot of light very quickly (Schalk 1990). Experience has shown that for healthy growth, they must be in full daylight for between 3 and 5 years (Vera 2000). Because of the growth rate, which is not paralleled by any other species of tree, in very light conditions Wild cherry can stay well ahead of other shade-tolerant species such as beech, hornbeam and sycamore, if it has a head start of 3–5 years' growth. Wild cherry exhibits fast growth during the first 30 years, after which the growth rate decreases. Due to this decreasing growth rate in the later stages of its life cycle, the risk of competition becomes evident. Shade-intolerant species such as Wild cherry show lower capacity to adapt their architecture and phenology and survive in light-limiting environments in the understory compared to more shade tolerant species. Although Wild cherry reaches ages of up to 80 years and more, it is generally replaced by climax tree species (e.g., the beech, *Fagus sylvatica* L.).

In standing trees, larger branches, limbs and other knot indicators are the largest group of log grade defects. Stem diameter and timber price per m^3 are increasing with decreasing crown base, i.e., increasing crown length (the larger the log, the better), but the volume of clean bole without any large knots is decreasing (Spiecker 2006). Pruning is a solution of these two contradictions when the bottom part of the crown of Wild cherry trees is removed. Natural pruning and the crown base height at a given stage of tree growth will depend on how the related live crown size controls diameter growth, and thus the height-diameter ratio and the duration of knot occlusion/knot depth (see Wernsdörfer 2005). Larger branches are exposed for a longer time to exterior influences, as the duration between branch necrosis and occlusion approximately increases with branch diameter (see Volkert 1953). Similar to larger branches, more inclined branches are reported to be more susceptible to rot (see Erteld and Achterberg 1954, Wernsdörfer et al. 2005). It must be noted that Wild cherry very often shows an insufficient qualitative value of production due to poor form caused by frequent forking and sinuous stem form (Rotach 1999). Stem form and forking of Wild cherry could be estimated as the dominance of stem axis (Ducci et al. 2006) whereby the main central stem of the plant is dominant over (i.e., grows more strongly than) other side stems, and on a branch, the main stem of the branch is further dominant over its own side branchlets. Growing away from the stem, the branches also receive more light than would a bundle of branches lying close to the stem and pointing upwards (Mattheck 1998). The number of branches per whorl in Wild cherry is significantly correlated with branch angle (Ducci et al. 2006); on the clones with a large number of branches are more likely to have branches that grow horizontally. Furthermore, Schulze et al. (1986) concluded that generally only acrotony (i.e., the privileged localization of sibling shoots in the subapical zone (distal part) of a parent shoot: Barthélémy and Caraglio 2007) coupled with hypotonic branching (the privileged repartition of sibling shoots on the basal position of a slanted or horizontal parent shoot: Troll 1937) is capable of developing a permanent and dominating canopy. In relation to that, a lower number of small dormant buds at the shoot base without a subtending leaf visible with the naked eye can be regarded as a fairly good measure for shoot vigour (Harmer 1989, Buck-Sorlin and Bell 2000, Petrokas 2008a).

An account of studies in Germany to find the best way of growing high-value Wild cherry is given by Spiecker (1994). The results indicate that Wild cherry reacts very strongly to varying water supply and to release. Annual basal area increment is closely related to growing space, and the supposed limit of minimum spacing (the diameter of a growing space circle) is at diameter at breast height multiplied by 25. The '5–10–20' rule-of-thumb in beech/cherry stands of Germany bordering on Luxembourg and France is (Wilhelm and Raffel 1993): never release cherry until self-pruning has reached 5 m height, release cherry before the clear stem is 10 m long, and maintain at least 20 m between crop trees. Pure stands are not advised as Wild cherry retains dead branches and must be pruned in order to produce high-value timber. Furthermore, rapid stem height increment during the first years following plantation is important to reduce the number of pseudo-whorls in Wild cherry (Santi et al. 1998). The pruning of young Wild cherry trees should be done moderately (more than a half of the crown should be left) when the bottom part of the crown is in the shadow zone of the crown layer, not earlier (Kupka 2007). This is done approximately every three years for a total of fifteen years. By pruning early, the amount of branch-free hardwood is increased and therefore more valuable for veneer. Another pertinent part of the management for cherry trees is removal of the dead branches to prevent disease. Risks such as rot and competition from climax species increase with the age of the tree. Usually, the maximum age of a cherry at harvest is 80 and the desired dbh – a maximum of 60 cm. Rots are the main problem in cherry, viz. branch-stem rot, root-stem rot, and wound stem rot; of these, branch-stem rot is the most dangerous. Wild cherry is subject to two major diseases, viz. anthracnosis, a fungal (*Blumeriella jaapii*) disease of leaves (the worst sanitary problem of Wild cherry in France: Santi et al. 1998), and bacterial canker caused by *Pseudomonas syringae* with three distinct pathovars, namely pv *syringae*, pv *morsprunorum* and pv *avii* (de Cuyper 2008). Aphids (*Myzus cerasi*) bend apical stems and affect stem form and straightness. Timber trees tend to be much less susceptible to bacterial canker, therefore ensuring that trees are of a timber type is essential for forestry purposes. In addition, Wild cherry must be protected against browsing and fraying by roe deer, but is not barked by red deer. Also it is affected by being nibbled by voles, mice and other wild animals.

Wild cherry is often mentioned as a potential alternative to poplar for the afforestation of abandoned and set-aside farmland (de Cuyper 2008). Increasingly planted as a timber tree, it is easy to establish and for a broad leaved tree it has a relatively short rotation or growing life and may become senile by 60. The wood of Wild cherry has good physical properties (Palm et al. 2005). In hardness, it is similar to birch,

while its bending strength is slightly greater than that of oak. In appearance, it tends to vary considerably. Sometimes, the boundary between sapwood and heartwood is difficult to detect. The sapwood is narrow and yellowish-white to light red in colour. The heartwood is yellowish-red to light reddish-brown. Greenish streaks sometimes appear in the wood. Exposed to the light it acquires a warmer and darker reddish hue reminiscent of mahogany. Planed surfaces acquire certain lustre. Straight-grained cherry is easily split but wood with an irregular grain structure is hard to split. The timber is easy to saw and dries quickly. Slow drying can reduce warping and improve colouring. Cherry wood is unstable in varying moisture. Easy to work with, medium wear on tools. The wood is suitable for steaming and bending, on a par with beech. The heartwood is comparatively resistant to decay. Good glueing properties and good results when finished. It is used for turnery products, furniture, veneers, decorative panelling, and pipes; good firewood with fragrance of blossom as burns. The major problems of cherry wood, which can reduce the processing yield and the quality of the final product, are the numerous knots (cherry is characterized by high pruning needs), the presence of green streaks, the gum pockets (Nocetti et al. 2008), the deviation of grain, and the frost cracks (Hemery et al. 2008).

A breeding program on Wild cherry in Greece is aimed at wood production (Aravanopoulos et al. 2008). Its objectives: state-wide phenotypic selection of plus-trees for wood production, grafting and tissue culture of elite trees, creation of an ex-situ clonal bank, determination of genetic diversity and DNA fingerprinting of elite material, comparison of results with a pool of domesticated cultivars of the same general geographic origin. Population evaluation is based on the phenotypic quality of individuals within populations (tree height, diameter, stem form, strength of apical meristem, absence of insect or disease problems, absence of frost related problems, lateral branch angle and diameter, etc.), and on selected plus-tree amenability to macro and micropropagation. France (the leading country in breeding of Wild cherry in Europe) confirmed the value of three of the cultivars – 'Ameline', 'Monteil' and 'Gardeline' – in 2006 (INRA press service 2006). To demonstrate precisely and rigorously the differences in behaviour between cultivars, and the stability of performance in different soils and under different climates the traits taken into account at the 45 comparative plantations of vegetatively propagated 403 plus-trees were: growth height and diameter – synonymous with high yield as well as good local adaptation; tolerance of cylindrosporiosis – this fungal disease causes leaf loss which inhibits diame-

ter growth; trunk straightness – a condition for satisfactory yield; thinness of branches compared with the trunk – branch thickness is closely linked to that of the trunk, but it is possible to breed individuals with a more advantageous branch diameter–trunk diameter ratio; the proportion of heartwood – it is preferred by industry; the stability of performance at all sites – this very important trait guarantees a good potential for the adaptation of a variety under varied ecological conditions, and hence satisfactory hardiness. Those cultivars must be planted on soils suited to the Wild cherry, but the plantations will be managed more intensively than those achieved with more "classic" plant materials (classified stands or seed orchards): lower planting densities (250 to 300 plants/ha instead of 500 to 600 plants/ha), more regular monitoring for shape pruning and general pruning: these more frequent operations than for a traditional plantation will focus on a smaller number of trees and take place during a shorter period because of the strong growth of these varieties. Furthermore, where water may be in short supply during summer, plantations should be established using seedlings rather than plantlets from micropropagation, as seedlings will develop a better tap-root system (Ducci et al. 2006). The pseudo-fasciculate root system obtained via micropropagation or cutting is better suited to alluvial or relatively deep sandy soils where water supply is constant.

Clonal varieties of Wild cherry are probably the best suited to large spacing plantations, and clonal selection is always one of the best selection strategies because it uses all genetic variability, additive and non-additive. Theoretically, when vegetative propagation techniques (grafting, cuttings, micropropagation etc.) are used, the complete genetic variance is transferred from the ortet to ramets (Ducci et al. 2006). The partitioning of genetic variance components in the experiment by Muranty et al. (1998) showed that additivity is the main mode of action of the genes that control the selected traits, but the dominance part is not negligible. The ratio of additive to global genetic variance was always higher than 0.6 but often smaller than 0.8 for the large stem height increment, girth increment and cherry leaf spot susceptibility. Thus clonal varieties would offer further genetic improvement in comparison to material produced in seed orchards. For most traits, estimated expected genetic gains with clonal varieties were actually larger than those expected from seed orchard (Muranty et al. 1998).

Vegetative propagation by cuttings is an effective way to capture genetic gain from selected trees and produce large numbers of planting stock for reforestation, agroforestry or horticultural programmes. According to Dick and Leakey (2006) juvenile cuttings

of *P. avium* rooted well (65% and 77% rooting for hard-wood and softwood shoots, respectively), while mature cuttings rooted poorly (4% and 7%, respectively). The cuttings were originated from juvenile sucker shoots of the current and previous year (types 1–2), and mature crown shoots (current year's lateral 'long-shoots' and multi-year terminal 'short shoots' – types 3–4). Cutting types 1–3 were single-node leafy cuttings, while type-4 cuttings were multi-nodal but with only one leaf retained. It is concluded by the authors that (1) after shoot type and tree number, leaf abscission was the primary factor associated with rooting; (2) cutting mortality occurred as a result of leaf abscission or through leaf or stem rotting; (3) cutting length was the second most important morphological variable fitted (i.e., longer cuttings rooted significantly better than shorter cuttings); (4) initial leaf area on the cuttings was the third most important factor significantly associated with rooting, and the relationship was positive. In the experiments with root cuttings of *P. avium* carried out by Ghani and Cahalan (1991) best results were obtained when cuttings were inserted with the proximal 2–3 cm exposed to the air; all lengths and diameters of root cuttings were successful (i.e., produced at least one sucker), and all successful cuttings produced roots at their distal ends.

Wild cherry is more common in grazed, park-like landscapes than in closed forests (Vera 2000), along moist river valleys (in North and South Italy: Ducci et al. 1988), by stream-sides in limestone areas (in Ireland). It grows as solitary trees or in small groups, more often as a minor admixture to broad-leaved forests (oak, hornbeam-oak, beech or beech-hornbeam) as well as on the outskirts of glades (Chukhina 2008), where direct sunlight is assured. It seems to grow best among beech, and in woods where the stem is drawn up to a good height before its crown expands (Elwes and Henry 1913); exposed sites should be avoided (Pryor 1985). Large gaps with 25-60 m in diameter are required to establish the natural or artificial regeneration of Wild cherry in the mixed stands of mesic broadleaved forests (Höltken and Gregorius 2007, Esen and Erdogan 2008). Minimum requirements for the productive tree growth of *P. avium* (after Russell 2003 and Reisner et al. 2005) are listed in Table 2. Wild cherry prefers drier climates, neutral to calcareous, fertile soils. It is indifferent to the geological nature of the soil, growing equally well on calcareous, gravelly, or sandy soils. Deep, well-drained, gravelly to sandy loam soils over limestone are best for Wild cherry (Bean 1976-1980, Rieger 2006). Flooded or wet, heavy clays slow growth and reduce productivity. Green manuring crops – bean, pea, red clover and white clover – are grown in cherry tree basins to improve soil texture and fer-

Table 2. Minimum requirements for the productive tree growth of Prunus avium. After Russell (2003), Reisner et al. (2005)

Criteria	
Altitude range	0–1700 m
Latitude range	30–61° North
Precipitation / year	580–1800 mm
Mean annual temperature	6–14°C
Mean maximum temperature of August	< 18–30°C
Mean minimum temperature of January	> –8–4°C
Light range	Sun to partial shade
pH range	6.6–7.8
Soil texture [1]	Medium, medium fine, fine
Water regime [2]	Dry, semi-wet
Soil type	Arenosol, Cambisol, Chernozem, Fluvisol, Lithosol, Luvisol, Rendzina, Vertisol
Minimum soil depth available for root growth	> 1 m
Minimum soil water capacity of the 1 m of soil	100 mm
Frost	Tolerant

1) Definition of the soil texture classes:
- coarse = clay < 18% and sand > 65%
- fine = 35% < clay < 60%
- medium = 18% < clay < 35% and sand > 15%, or clay < 18% and 15% < sand < 65%
- medium fine = clay < 35% and sand < 15%

2) Definition of water regime (dominant annual average soil water regime class of the soil profile):
- dry = not wet within 80 cm for over 3 months, nor wet within 40 cm for over 1 month
- semi-wet = wet within 80 cm for 3 to 6 months, but not wet within 40 cm for over 1 month
- very wet = wet within 40 cm depth for over 11 month
- wet = wet within 80 cm for over 6 months, but not wet within 40 cm for over 11 months

tility (Jindal et al. 2008). The potential distribution area of Wild cherry covers an area of 296'335 km^2 = 18.2% of the European arable land (Reisner et al. 2005). The potential distribution area mean the potential growth areas on arable land (overlaying potential tree growth areas with arable land). However, Wild cherry seems to be very difficult to establish on former arable land, often with unknown reasons (in Sweden: Albinsson 2009).

Reproduction considerations

Plants lack any central controller for morphogenesis or behavior (Oborny 2003). Indeed, adaptation to the environment seems to hinge on the opposite of centralized control: interactions between individual modules, such as flowers, leaves, and internodes, or groupings of these components, such as metamers or shoot units and branches. Each module may be semiautonomous, which may be expressed through phe-

nological behaviour (Hallé 1986). The highest degree of module independence is achieved by clonal plants, in which each module can develop a self-supporting shoot and root system, and thus, the genetic individual (genet) can get fragmented into independent physiological individuals (ramets). Survival and reproduction of a single module is relevant only to the extent at which it increases or decreases fitness of the whole plant individual. Fitness of a genotype (a type of reaction norm) depends on the performance of the whole plant individual in its environment. The environment has a twofold role in any case of adaptive plasticity: on one hand, it induces a phenotype; on the other hand it selects for or against that phenotype. Fitness relies on the correlation between the inducing and selecting environment, i.e., on the reliability of environmental cues. A time lag between induction and selection can seriously limit the adaptive value of plasticity, or may even favor rigid development. The timing of vegetative and generative phenological events in spring is used to discriminate among genotypes within Wild cherry (Ducci and Santi 1997) since in most tree species it has a high broad-sense heritability (often >0.9). The timing of knot occlusion could be estimated as natural pruning (Petrokas 2008a). Bud burst asynchrony is defined at the first occurrence of last stage taking into consideration the limiting stages of burst progress between tree annual shoots of strongest axes of sequencing orders (Petrokas 2008b). Flowering synchrony between Wild cherry accessions is expressed as differences in date of full bloom by recording the share of fully opened flowers every 48 hours during the whole flowering period (de Cuyper 2008). It has to be taken into account that fully opened flowers are only receptive for 38 hours and that the pollen in the pollen bags of bumble bees are viable during 12 hours. As regards the timing of shoot tip, leaf or fruit coloration, although it is well established that the green and yellow colors of leaves are attributable to chlorophyll and carotenoid pigments, respectively (Taiz and Zeiger 2002), both carotenoid and anthocyanin pigments can contribute to the expression of red in leaves (Lee and Gould 2002, Schaberg et al. 2008). Exposure to an array of stressors, including drought (Balakumar et al. 1993), low temperatures (Krol et al. 1995), wounding (Ferreres et al. 1997), and pathogen infection (Dixon et al. 1994) have been shown to elicit anthocyanin biosynthesis. This buildup of anthocyanins following stress exposure raises the possibility that anthocyanins may function, in part, to prevent or offset stressinduced damage.

Sequential reiteration (Oldeman 1974, Barthélémy et al. 1991) is the complete or partial repetition of a tree's crown, originating from an adventitious or proventitious bud. The distinction between adventitious and proventitious bud seems to be essential here. The proventitious buds are characterised by being connected to the pith and have potential as they are free from inhibiting factors correlation. They become covered by the bark, but move out with the cambium so that they are always near the surface and retain connection back to the pith by means of a stele – a bundle of water-conducting tissues also known as a bud trace. Guinier et al. (1947) was definite that proventitious buds on the stems "remain apparently lifeless" but "give rise every year to a few cells, which form a very small shoot embedded in the wood and the shoots bark. The bud finds itself cut off and can maintain itself on the surface of the shoot, even there is an increase in diameter." Poskin (1939) assimilated proventitious buds to a resting phase (period of dormancy) of the bud prior to flushing, this phase is reactivated by "the abundance of sap and a strong light influence. This evolutionary faculty is conserved during early years but reduces progressively as the tree becomes old." On a stump it gives rise to proventitious shoots, which, due to their growth from a bud at the base or old roots of a tree and their close relationship with the stump are less exposed than the adventitious shoots to physical damage (by snow, trampling by wildlife, by windbruch). Adventitious shoots produce stems capable of supporting a good growth for a limited period before most of them disappear because they failed to establish a conductive system. Adventitious shoots show very strong apical dominance. They are known as water sprouts that form on stems and branches, and suckers, which grow from a bud at the base or roots of a tree. When they are in contact with the soil, they have the rooting ability and become independent to the mother tree thus differing from "stump or coppice shoots" which develop from a stem. Most commonly, water sprouts follow sudden exposure to increased light levels, for instance, after a forest has been released via thinning or selective harvesting. Newly formed water sprouts do not penetrate deeply into the interior wood, but if allowed to grow, can become sizable limbs, significantly lowering lumber grade and value. Limbs are identified by their tendency to grow nearly parallel to the main tree stem and by an abrupt increase in diameter at the base. The bark of these limbs retains a smooth or juvenile appearance to a much larger size than primary branches. In shelterwood cuttings of even-aged stands, large-crowned trees of all species can be left in open conditions without danger of water sprouts developing (Godman 1992). In uneven-aged stands, if crowns are released gradually by maintaining the proper stand structure, water sprouts are seldom a problem.

Suckering (clonal regeneration) is a means of vegetative propagation which allows some plants species to propagate, and possibly to spread, by producing adventitious shoots from the root system. Suckers (Bellefontaine et al. 2002) generally originate on the young structures of the pericycle (if they happen to arise from an old root, it will be from the peripheral cortical parenchyma; in that case it will subsequently have its own inward connection); the sucker is therefore a stem anatomical structure which are generally from lateral or superficial roots and which can only be adventitious. The extent of suckering may significantly influence the genetic structure and reproductive ability of Wild cherry populations. Suckering leads the whole Wild cherry populations (clump stands) being made up of one or a few genetically identical clones (White 1978, Fernandez et al. 1994, McLellan et al. 1997). In the study of clonal structure and recruitment in British Wild cherry Vaughan et al. (2007) used simple sequence repeat (SSR) variation to examine the relative frequency and distribution of vegetative derived Wild cherry in two ancient woodlands subject to contrasting management regimes. It was found that spatial genetic structure in Wild cherry is amongst the strongest reported for tree species and that management regimes significantly influence population structure. Suckering accounted for a significant proportion of Wild cherry recruitment, with approximately half and two-thirds of trees belong to clonal groups in the managed and unmanaged populations, respectively. Clonal genets in the unmanaged site contained significantly higher numbers of significantly smaller ramets and, on average, covered less than half the area of clonal groups at the managed site. Vaughan et al. (2007) suggests that a policy of non-management, especially following winter storms, may help maintain genetic diversity of Wild cherry through increased levels of both sexual and clonal recruitment.

The clonal growth strategy has a potential impact on mating patterns and may affect reproductive success both positively and negatively (Handel 1985). A negative effect of clonal growth on reproductive success is geitonogamy, i.e., self-pollination between flowers within a genet (Eckert 2000). In self-incompatible plants such as Wild cherry, geitonogamy may lead to the wastage of pollen deposited on incompatible stigmas and stigma clogging by incompatible pollen, resulting in reduced fertilization (Waser and Price 1991, Harder and Barrett 1995). On the other hand, a positive effect of clonal growth on reproductive success is floral display, which attracts pollinators and increases mating opportunities (Klinkhamer et al. 1989). Pollinators may recognize floral display in various spatial scales, which can correspond to spatial aggregations of flowers within inflorescences, ramets, and ortets. If pollinators respond to floral abundance in a large spatial scale, as in genets (Thompson 2001), clonal growth will increase pollinator visits and reproductive success (Kato and Hiura 1999). Therefore, clonal growth potentially has both positive and negative effects on reproductive success owing to floral display and geitonogamy, respectively (Mori et al. 2009).

Gametophytic self-incompatibility in *P. avium* was attributed to a multi-allelic single locus (S-locus) by Crane and Lawrence (1929). In this type of self-incompatibility, pollen tube growth is arrested in the style and fertilization fails to occur when the S-allele in the haploid pollen grain matches one of the two S-alleles expressed in the diploid pistil (Lewis 1942, de Nettancourt 1977). Male determinant of gametophytic self-incompatibility in *P. avium* – S haplotype-specific F-box protein gene, SFB3 (Yamane et al. 2003, Ushijima et al. 2004, Sonneveld et al. 2005). The existence of gametophytic self-incompatibility in Wild cherry may restrict the number of potential males in a planting because in addition to self-incompatibility, there is a high degree of cross-incompatibility: 38 cross-incompatibility groups have been identified in *P. avium* (Stanys et al. 2008). The alleles S_4 and S_5 are absent in Wild cherries, whereas S_7, S_{10} and S_{12} to S_{16} are frequent in Wild cherries but rare in sweet cherry cultivars grown for their fruit, S_{17} to S_{22} – unknown in sweet cherry cultivars (de Cuyper et al. 2005). If the incompatibility alleles are known for each cultivar, they can be arranged to adjust the spatial design of the planting to the phenologic and gametophytic cross-compatibility of the selected genotypes (after de Cuyper 2008). The universal donor cultivars – cross-compatible with all varieties (e.g., 'Orleans 171' – S_7S_{10}, 'Hrebnickio1' – $S_{12}S_{16}$, 'Rita' – S_5S_{22}) – can be planted with any cultivar to get good fruit set provided by their flowering period overlaps (see Bekefi et al. 2003, Tobutt et al. 2005, Stanys et al. 2008). A few sweet cherry cultivars are reported in the literature to be naturally self-compatible. These include the Spanish cultivar 'Temprana de Sot' and its sport 'Cristobalina' (Wünsch and Hormaza 2004a, b), and the Italian cultivar 'Kronio' (Calabrese et al. 1984), named after the mountain in Sicily in which it was collected. Despite historic links between Spain and Sicily and the presence of S6 in both 'Kronio' and 'Cristobalina', the nature of the self-compatibility of these two early ripening cultivars is different (Marchese et al. 2007). Spontaneous self-compatible cherries are particularly well suited to areas where poor weather during pollination limits bee flight and thus pollination and fruit set. It is possible that self-compatibility in cherry may have been indirectly selected by man. If flowering is very early, and

few pollinators are available, then self-incompatible early flowering varieties would not crop well. So selection for reliable cropping in such types may have led to selection for self-compatibility.

Wild cherry, a partially asexual self-incompatible forest tree, shows heterozygote excess, which is a poorly studied phenomenon (Stoeckel et al. 2006). The excess or deficit of heterozygotes observed within a population, varies markedly with mating systems and selection regime, i.e., whether selection favours homozygotes or heterozygotes (Wright 1969). Theoretical and empirical studies have found heterozygote deficit to be due either to artefactual (null allele, short allele dominance, inappropriate sampling – population admixture Wahlund effect) or biological (inbreeding, positive assortative mating, selection against heterozygotes) causes. The origin of heterozygote excess, in contrast, remains poorly studied. Insofar as heterozygous advantage exists, some members of the natural populations will be imperfectly adapted. This situation may arise because the heterozygotes cannot, under Mendelian inheritance, produce purely heterozygous offspring: they cannot breed true (Ridley 2003). A proportion of the population must therefore have the deleterious homozygous genotypes. However, in small sexual or self-incompatible populations, the fact that individuals cannot reproduce with themselves decreases the probability of creating homozygote offspring (Wright 1969, Balloux 2004). In the case of *P. avium*, 'Cristobalina' (S_3S_6), a spontaneous self-compatible cultivar grown in the Alicante Mountain area, has been shown to produce S_3S_3 homozygous seedlings by self-pollination (Wünsch and Hormaza 2004b).

Suggestions

High genetic diversity, high heterozygosity, low spatial genetic structure, high pollen flow, high polyandry and low clonal propagation indicate diversity and thus adaptive potential of Wild cherry (Jolivet and Degen 2008). The genetic diversity of *P. avium* has been shown to be weakly spatially structured, the geographic differentiation – low (Mariette et al. 1997, Mohanty et al. 2001). It is becoming increasingly important to conserve the existing variability in the wild stands of this species scattered through most European and some Asian countries, especially due to the progressive narrowing of the genetic base (Wünsch and Hormaza 2002), as the potential economic interest is limited in good fruit quality cherry varieties (see Iezzoni et al. 1990) and self-compatible cultivars derived from a single cultivar 'Stella'. Furthermore, the conservation of unique natural genotypes (e.g., spontaneous self-compatible or homozygous S-genotypes)

is of special importance. Gametophytic incompatibility system in *P. avium* exhibits high polymorphism at the incompatibility controlling S-locus therefore individuals with rare alleles have a higher probability to successfully pollinate others than individuals with more frequent alleles (see Schueler et al. 2006).

The establishment of local populations of Wild cherry including several generations is likely due to its ability to develop mixed reproductive strategy involving clonal regeneration. Owing to its considerable capacity of a rapid vegetative propagation through root suckers, Wild cherry behaves as a colonizing species of initial succession stages (Gömöry 2004) and during progressing succession of the local disturbance (see Höltken and Gregorius 2007) it may become a component of climax or close-to-climax mesophilous forest ecosystems (see Ducci and Proietti 1997). In beech or oak stands, which are generally quite dense, there is rather little space for light-demanding Wild cherry, therefore suckers, which can use the root systems of the parent tree at initial life stage, have a higher survival probability than seedlings. The principle is thus to exploit the suckering ability of Wild cherry and manipulating factors affecting sucker production to obtain the targeted results for its regeneration maintenance. Therefore, vegetative multiplication of Wild cherry from root suckers is a method that can be used in forestry due to the following exformation:

1. Generally, the straightest growing deciduous trees without forest shade pressure are those, which are most light-demanding. Similarly, adventitious sprouts follow sudden exposure to increased light levels and show good growth and very strong apical dominance – they are more light-demanding compared to the proventitious shoots, which are formed from the buds connected to the pith.

2. The ability to survive under local stresses can be fixed by vegetative propagation through adventitious suckers; therefore plantlets from the adventitious bud should be used as a reproductive material. In addition, for species that can reproduce both sexually and clonally sexual reproduction promotes recombination, and clonal reproduction preserves successful combinations.

Ontogenetic ageing (ageing of meristems, which is genetically programmed – after Fortanier and Jonkers (1976)) of the stock plants needs to be understood if plants are used for vegetative propagation. In analyzes of phenotypic variation in plants genetically programmed ontogenetic changes in form and function (e.g., metamorphosis) can be similar in pattern to environmentally induced changes (plasticity). However, the metamorphosis is subject to plasticity (Diggle 2002), the timing of ontogenetic changes is subject to environ-

mental influence (Allsopp 1967, Lee and Richards 1991, Jones 1995, and examples given by Alpert and Simms 2002). Experiments that controlled for both leaf position (architecture, *sensu* Diggle 1995) and environment, demonstrated that although environment (temperature), leaf position, and their interaction all contribute to variation in leaf traits, position has by far the greatest effect: this variation is primarily the result of a fixed ontogenetic progression of leaf types. Furthermore, the growth pattern of a tree determines the whole sequence of its development: "In this sequence, leading from axis 1 to the ultimate axis category, following the specific branching pattern, each branch is the expression of a particular state of meristematic activity and the branch series as a whole can be considered to be tracking the overall activity" (Barthélémy et al. 1991). In conclusion, ontogenetic variation in phenological behaviour could be used to quantify the stability of performance in different soils and under different climates subject to contrasting management regimes – this very important trait guarantees a good potential for the adaptation of an accession of Wild cherry under varied ecological conditions, and hence satisfactory hardiness (see Hallé 1986, Beaudet and Messier 1998, Sundarapandian et al. 2005, INRA press service 2006, Barthélémy and Caraglio 2007). The timing of vegetative and generative phenological events (e.g., knot occlusion, bud burst asynchrony, flowering synchrony, shoot tip and leaf coloration, susceptibility to anthracnosis, fruit ripening) occurring as the result of ontogenetic variations in the architectural traits of crop tree axes (e.g., privileged localization or repartition of sibling shoots, number of basal buds without a subtending leaf), leaves (e.g., leaf shape and size, length of petiole and length of blade ratio), flowers (e.g., season of flowering, self-compatibility) or fruits (e.g., fruit shape and size, length of stalk and length of fruit ratio) could be monitored and described and the role of management (or environment) influences in determining these events could be related. Management influences here refer to the socioeconomic attributes of trees (see Raintree 1991), such as stem form and forking, branch number per whorl, branch angle, height/diameter increment of stems, the ratios of crown diameter and diameter at breast height, total height and length of living crown, or stem diameter (just above the pseudo-whorl) and strongest branch diameter, the distances from the stems of crop trees to the stems of neighbour-trees multiplied by two and divided by the breast height diameter of these crop trees (see Spiecker 1994).

Management is an intervening variable between the biophysical attributes of trees and the socioeconomic expression of those attributes (Raintree 1991). An ideotype denotes a set of attributes that are appropriate to a particular end use, a particular management system, and a particular set of site conditions. Donald and Hamblin (1976) proposed that plants could be divided into 'isolation,' 'competition', and 'crop' ideotypes, each with a distinct competitive strategy, and each one appropriate for a particular cultural system.

The 'competition' ideotype would be the model most appropriate for plantations of high-value species, such as Wild cherry, where the aim is to produce large-diametered trees yielding high-grade logs. Mortality of suppressed trees is of little consequence in this situation, if the remaining trees are of the highest quality and are growing rapidly. The silvicultural goal may be just a few exceptionally valuable trees per hectare at the end of the rotation. Trees of this ideotype arenot the forestry equivalents of agricultural field crops, but, in case of Wild cherry, they require a high level of inputs.

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ПРЕДПОСЫЛКИ ДЛЯ РЕПРОДУКЦИИ ЧЕРЕШНИ (*PRUNUS AVIUM* L.): ОБЗОР

Р. Петрокас

Резюме

Черешня (*Prunus avium* L.) благодаря ощутимой масштабности рассеивания или быстрого размножения через корневую поросль на изначальных сукцессионных стадиях ведет себя как вид-колонист. С другой стороны, по ходу прогрессирующей сукцессии местного нарушения она становится составной частью климаксных или близких к климаксным экосистем мезофильных лесов. Там, где она распространена, прекращение лесовостановительных работ, в особенности после зимних бурь, через повышение уровней генеративного и вегетативного возобновления способствует более успешному сохранению её генетического разнообразия. Объектом обзора является состояние исследований по влиянию хозяйствования на репродукцию черешни в границах её фенологического поведения. Мониторинг генеративного и вегетативного фенологического поведения черешни, как результата онтогенетических вариаций в признаках деревьев и их частей, должен способствовать определению влияния окружающей среды или хозяйствования на это поведение. Предпосылки, касающиеся исследований репродукции черешни, в обзоре представлены для дискуссии.

Ключевые слова: влияние хозяйствования, *Prunus avium*, репродукция, фенологическое поведение.