Commentary
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Michurin's legacy to biological science

Today, Ivan Michurin is remembered mostly for the discredited Michurinian genetics. However, this great horticulturist and Russia's 'Luther Burbank', in the course of more than 60 years in plant breeding, not only produced more than 300 strains of horticultural plants but also elaborated many theoretical principles and practical methods. Over the past several decades, however, Michurin's name has become inextricably linked to that of his most notorious disciple – TD Lysenko. Of late, Michurin's name has been slowly reappearing in scientific literature (Flegr 2002; Ivanyi 2003; Liu 2006; Liu *et al.* 2010). The main reason is that it has been shown that some epigenetic changes can be passed on to the offspring in ways that appear to violate Mendelian genetics. In addition, it has been shown that the plant genome is remarkably unstable, capable of undergoing change and generating variability during very early stages of development, and there is increasing evidence in support of Michurin's methods of mentor grafting and mentor pollination.

The basic principle of Michurin's operations was the change in heredity induced by environmental changes in the early development stages of plants. He proved by experiments that the acclimatization of plants is indeed possible, but 'only by planting the seeds'. He made great use of grafting as a means of influencing and improving immature plants, and showed that plants could be altered by grafting in a sufficiently early phase of development. He emphasized repeatedly that young plant organisms were highly susceptible to the influence of environmental conditions. The young organism resulting from the cross of the initial parental pairs is distinguished by its destabilized heredity and hence possesses great plasticity. It should be noted that Michurin's assumption is not only consistent with Darwin's and Burbank's ideas but also supported by recent findings. Throughout his career, Darwin consistently linked the cause of variation to changes in the environment. Recently, it has been shown that adaptive phenotypic plasticity is generally expressed for plants exposed to an environmental perturbation during very early stages of development (Amzallag 2004). Several other instances have also been documented in which the genome does alter in response to the environment, and this change usually occurs in the early stage of development (Durrent 1962; Cullis 2005). It should be noted that Michurin's idea was supported by Konrad Lorenz, who later proposed that imprinting occurs in 'critical periods', which are limited and severely restricted to the animal's very early life (cited in Tzschentke and Plagemann 2006). Now it is known that nutrition in early life might influence adult phenotypes through DNA methylation. On observing agouti mice born to mothers that were fed diets containing different amounts of methyl donors, one will see mice with coats of different shades of colour, from yellow to brown to almost black (Vercelli 2004). Cropley *et al.* (2006) reported the effects of specific timing of maternal dietary methyl supplementation on the coat colour of the offspring, and found that maternal supplementation only during mid-gestation substantially affected offspring coat colour, and this effect is inherited by the subsequent generation.

Michurin's most important contribution, in Vavilov's opinion, was that he promoted the idea of remote hybridization, he made very original attempts to produce new species of plants by cross-breeding them with other species and he demonstrated both in theory and in practice the correctness of that method (Popovsky 1984). Michurin was one of the first investigators in the history of plant breeding to use not only inter-specific but also inter-generic hybridization between such taxonomically remote species, and obtained dozens of valuable plant varieties. To cross species of plants that were least closely related, it is necessary to find ways and means to overcome the resistance to crossing. One of the important barriers to wide hybridization is rejection of pollen by a foreign style. Either the pollen is

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unable to germinate or the pollen tube is inhibited in the pistil before it reaches the egg. A thorough study of pollination biology in fruit plants enabled Michurin to introduce the method of mentor pollination to breeding, thus overcoming the difficulties in wide hybridization. Mentor pollination is the use of a small amount of pollen that is highly compatible with the seed parent, mixed with a large amount of pollen from the intended pollen parent to increase the chances of success in wide hybridization. Since this method was discovered by Michurin, it has been investigated by breeders as a possible tool to overcome incompatibility barriers both in self- and inter-specific incompatibility (Stettler 1968; Pandey 1977; Knox *et al.* 1987; Gaget *et al.* 1989; Wenslaff and Lyrene 2000). For example, obtaining blackthorn×plum hybrids was greatly facilitated by using a pollen mixture of different plum varieties (as compared with pollination by each plum variety separately). The cross sand cherry×plum only succeeded when plum pollen was mixed with myrobalan pollen (Yenikeyev 1965). In blueberry wide hybridization, when *Vaccinium elliottii* 'Oleno' was the seed parent, no hybrids were produced unless mentor pollen was utilized (Wenslaff and Lyrene 2000).

Inter-specific crosses that are normally difficult or impossible to obtain can also be facilitated by previous grafting between the intended sexual partners, which Michurin termed 'preliminary vegetative approximation'. The method of 'preliminary vegetative approximation' consists in the following: cuttings of 1-year-old hybrid seedlings are grafted onto a branch of the crown of a mature tree of a different species or genus. The grafted cuttings continue to develop in the course of the next 5 or 6 years under the constant influence of the tree to which they have been grafted, and by virtue of this they partially change their structure. When the first flowers appear on the grafted cuttings, they may be pollinated by the pollen collected from the flowers of the tree on which the cuttings grew. In a report published in 1925, Michurin described his innovation in the following words: 'I use this vegetative change as an auxiliary means to approximating two different plant species so as to obtain a sexual hybrid by crossing them in the future. This is the secret of my success in obtaining interspecific plant hybrids, such as crosses between the apricot and the plum, sweet and sour cherry…'. This method has been applied not only to fruit trees but also to annual plants. It is well known that wheat and rye are very difficult to hybridize. Hall (1954) found that only 2% to 3% of wheat flowers pollinated by rye produced seeds. However, of the 2897 wheat flowers borne by plants, which, as embryos, had been grafted onto rye endosperm, 400 (14%) gave seeds when pollinated by rye. Nirk (1959) reported the successful crossing of *Lycopersicon esculentum* with *L. peruvianum* by employing the reciprocal grafting of parent plants prior to hybridization. This method has also been used in wide hybridization of other plants (Evans and Jones 1964; Rao and Ram 1971).

Although Darwin was the first to put forward the concept of graft hybridization, he did not know under what conditions graft hybridization could be effected. One of Michurin's most notable achievements was his mentor grafting method, with which Darwin's 'unknown conditions' of producing graft hybrids could be revealed. This method involves the following: by grafting several scions taken from old strains of fruit trees onto the lower branches of a young seedling's crown, the young seedling acquires properties that it earlier lacked, these properties being transmitted to it through the grafted twigs of the old strain. He emphasized repeatedly that this method could be employed effectively only on young seedlings and not on old and long-established varieties. By this method Michurin produced or improved a number of new good strains. Later, Michurin's mentor grafting method was improved and applied to annual plants. In the last decades, several independent groups of scientists repeatedly showed that mentor grafting was a simple and effective means of plant breeding, and that graft-induced variant characteristics were stable and inheritable (Taller *et al.* 1998; Liu 2006). It should be noted that as early as 1933, Michurin deduced that the stock genes could be transferred into the scion and incorporated with the scion genes and *vice versa* (Michurin 1949). Recently, Stegemann and Bock (2009) demonstrated that plant grafting could result in the exchange of genetic information via either large DNA pieces or an entire plastid genome. This observation provides a nice confirmation of horizontal gene transfer between the stock and the scion. It should be mentioned that it was Michurin's work on graft hybridization that led Hasek to make the crucial decision to choose chicken embryo as his experimental model, which turned out to be crucial for the discovery of immunological tolerance (Ivanyi 2003). Michurin's work on graft hybridization also inspired animal breeders to investigate the effects of blood transfusion on hereditary traits, which was also known as animal vegetative hybridization (Liu 2008).

In his notebook, Darwin repeatedly mentioned Yarrell's law. This law was named for William Yarrell, a British naturalist and animal breeder. It maintains that a parent of an older breed will have more influence on the character of the offspring than a parent of a young breed (Darwin 1987). This law was later confirmed by Michurin, who found that old varieties of fruit plants possess a stronger capacity for transmitting their characters than young varieties. 'The older the plant chosen as a progenitor, the greater is the force with which it transmits its genes to the offspring, and conversely, if the plant is young, in its first year of bearing, and particularly if it is a hybrid of recent origin, its hereditary power reaches a minimum' (Michurin 1949). Recently, it has been shown that circulating nucleic acids occur ubiquitously and are bioactive in living organisms. Apoptosis is the most common form of cell death, continuing throughout life from early stages of embryogenesis to death. It has been documented that there is an enhanced apoptosis with increasing age. With the establishment that apoptosis is the most common form of cell death and that apoptosis is enhanced with increasing age, the ability of circulating DNA/RNA to be incorporated into gametes and expressed in the progeny, a mechanism exists for Yarrell's law (Liu 2009).

Although Michurin's name has become inextricably linked to Lysenko, a careful analysis of the literature reveals that there are many differences between them in either personal characters or scientific attitudes. Michurin was a man of touching enthusiasm and indomitable optimism, self-critical, talented, honest and industrious. Michurin recognized the significance of Mendel's laws and the existence of genes. In his *Selected Works*, Michurin wrote, 'I by no means deny the merits of Mendelian laws. On the contrary, I merely insist on the need to introduce amendments and addenda into it, for it is evident to everybody that his calculations are not applicable to cultivated varieties of fruiters…' (Michurin 1949). It is not surprising that Michurin's conclusions are different from Mendel's, because their experimental materials and research methods are quite different (table 1). However, Lysenko not only totally denied the significance of Mendel's laws and the existence of genes but also regarded Mendelian genetics as 'bourgeois science' and 'pseudoscience', and forced Soviet geneticists to accept Michurin's teachings or be banned from doing research.

Vavilov is one of the most distinguished geneticists and international scientists of Russia. The friendship between Michurin and Vavilov is well known. The two men first met in 1921, and Vavilov was greatly impressed with Michurin's achievements in fruit breeding. He requested a report from Michurin and induced the government to provide Michurin with an experiment station of his own and adequate funds. Michurin was deeply indebted to Vavilov for this help and praised Vavilov as 'a clever mind, a great scientist and a good soul'. The two men remained in contact for the rest of Michurin's life. Shortly before Michurin's death, Vavilov sponsored his election to honorary membership in the Soviet Academy of Science (Lang 1956). However, the relation between Lysenko and Vavilov was rather strained. In Vavilov's opinion, Lysenko was 'an angry man' (Darlington 1977).

Michurin's manner of work was vigorous and unconventional, and firmly directed to practical aims. His theoretical ideas emerge quite clearly from his writings, although often cast in the form of practical instructions or descriptions of methods. But he was always conscious of the need for a correct theory on which to work, and like Darwin, he based his ideas on the closest observation of nature. As for the man himself, we will let Michurin have the last word: 'I must say that I have spent all my life in the orchard and on the garden beds. During my life I have made a great many observations and studies of plant life. I have discovered hosts of new facts that still await their theoretical significance to be investigated by science. Those facts must certainly be thoroughly elucidated in detail from the theoretical standpoint' (Michurin 1949).

Table 1. Comparison of Mendel's and Michurin's works

	Mendel	Michurin
Experimental materials	Annual plants	Perennial plants
Main methods	Intraspecific hybridization	Wide hybridization and graft hybridization
Characteristics investigated	Qualitative	Quantitative
Focal point of research	Transmissional genetics	Developmental genetics

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