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In situ conservation and landscape genetics in forest species

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Abstract

Conservation of forest genetic resources is essential for sustaining the environmental and productive values of forests. One of the environmental values is the conservation of the diversity that is assessed through the amount of genetic diversity stored by forests, their structure and dynamics. The current need for forest conservation and management has driven a rapid expansion of landscape genetics discipline that combines tools from molecular genetics, landscape ecology and spatial statistics and is decisive for improving not only ecological knowledge but also for properly managing population genetic resources. The objective of this study is to show the way to establish the safeguard of genetic diversity through this approach using the results obtained in sweet chestnut (*Castanea sativa* Mill.) that has provided a better understanding on the species genetic resources. In this respect, we will show how the information provided by different types of molecular markers (genomic and genic) offer more accurate indication on the distribution of the genetic diversity among and within populations assuming different evolutionary drivers.

Why to conserve plant genetic resources?

The approval of the Convention on Biological Diversity (CBD 1992) and the International Treaty on Plant Genetic Resources for Food and Agriculture (FAO 2001) constitute a response to the environmental degradation that is the direct results of human pressure on the ecosystem. Accordingly, it is necessary an integral system of conservation and sustainable use of the genetic resources that includes economical, social, political and ethical aspects.

Forest systems provide food, as well as a large number of non-food goods and services and shape, in great part, a landscape in which human footprint is enhanced. These types of services, which have intangible value, are "externalities". In this study we will try to show how the discipline of landscape genetics can contribute to safeguarding the forest genetic resources.

Biodiversity is defined as the variation of all living organisms at different levels: ecosystems, species and genetic diversity (Wilson 1988). In this context, genetic diversity is defined as the basis of all biodiversity and is widely considered as the main requirement for the long-term survival of species on an evolutionary time scale (Booy et al. 2000; Namkoong 2001). Conservation of such variability has become a renewed focus under the expectation that its loss could render populations and species less able to adapt to ongoing environmental changes (Mace et al. 2003; Jump and Peñuelas 2005). On the other hand, sustainability is defined as the use of natural resources without risking their exploitation by future generations (World Commission on Environment and Development 1987). For all these reasons, forest management can only be considerate as sustainable if it includes a suitable system of plant genetic resources conservation.

Conservation of forest genetic resources is, therefore, essential for sustaining the productive values of forests, maintaining the vitality of forest ecosystems and, thereby, for maintaining their environmental roles (Young et al. 2000). However, one of the greatest threat to forests and the diversity housed in them is the increasing pressure to which these forests are exposed from human management (Poffenberg 1996; Palmerg-Lerche 1999). Although it is inevitable that land use changes will influence forests structure, such changes should be planned to help ensure conservation as a major component in land use planning and management strategies. Currently, different degrees of management can be found in forest trees, from natural forests without intervention (for example *Araucaria araucana* (Mol.) K. Koch, *Nothofagus* sp., *Abies pinsapo* Boiss. and *Taxus bacatta* L.) to highly altered systems (*Olea europaea* L., *Quercus* sp., *Juglans reggia* L. and *Castanea sativa* Mill.). This means that strategies to preserve these gene pools have to be adapted to each particular case.

Furthermore, problems related to the conservation and use of these genetic resources are especially complex, not only because genes must be retained, but also because we have to maintain genotypes (set of co-adapted genes that are the result of natural and artificial selection) and evolutionary processes that have led to this diversity (Namkoong and Ouédrago 1997).

Different approaches to evaluate genetic diversity

The CBD and the Treaty have led to initiatives, at different levels, that seek to translate its principles into actions considering national and regional realities. In Spain in 2006, the Spanish Strategy for the Conservation and Sustainable Use of Forest Genetic Resources was presented (MIMAM 2006). This Strategy is currently being developed through several national plans. In addition, in 2010, the Ministry of Science and Innovation established the ten most important research topics in which Spain must be leader in 2020, being the genetic resources one of them.

In most forests with high environmental values, there is a better understanding of their specific composition and the ecosystems in which they are related rather than the degree of genetic diversity of species they contain (Young et al. 2000). The knowledge of such diversity is particularly relevant in the case of woody species, which have been named "ecosystem engineers" (Wright and Jones 2006; Shackak et al. 2008).

The concept of landscape ecology was developed at the end of the 1930s. The objective of this approach is to have an advanced comprehension of ecological processes and landscape function (Farina 2000). Landscape ecology emphasizes the ecological effects of the spatial and temporal patterning of ecosystems (Turner 1989, 2005).

Currently there is growing interest in combining the tools of molecular genetics with the principles of ecological biogeography and landscape ecology (Manel et al. 2003; Latta 2006). Evolutionary processes are influenced by environmental variation over space and time, including genetic divergence among populations, speciation and evolutionary change in morphology, physiology and behaviour (Kozak et al. 2008). Studies on genetic structure in natural populations, including within and among population genetic diversity and genetic differentiation, have been a major topic in evolutionary ecology and genetics (Patausso 2009). In this respect, in the international literature there is a new and integrating approach in the study and management of natural resources: landscape genetics (Manel et al. 2003; Holderegger and Wagner 2008). This approach integrates the tools provided by molecular genetics and ecology with the new statistical tools such as geostatistics, maximum likelihood and Bayesian approaches (Wulder et al. 2004; Storz 2005). The aim is to provide information about the interaction between landscape features and evolutionary processes, such as gene flow, genetic drift and natural selection (Manel et al. 2003; Latta 2006; Storfer et al. 2007). Furthermore, it enables the spatial mapping of allele frequencies from one ore more species (or populations) and subsequently the correlation of such patterns with the current landscape (Storfer et al. 2007; 2010). In this respect, landscape environmental features (elevation, slope, etc.) can influence genetic structuring of populations at a regional level because they can affect gene flow and exert selection pressure (Gomez et al. 2005). Currently, a step forward in this discipline is the new field of landscape genetics of adaptive genetic variation that establishes the relationship between adaptive genomic regions and environmental factors, being prominent in plant studies (Holderegger et al. 2010).

An example that Landscape Genetics is a rapidly evolving field is the fact that in January 2012, the paper that first coined this term (Manel et al. 2003) has 520 citations according to Thomson Reuters web of science. In the same way, there has been an impressive increase in the number of publications on this subject in the last years: 6 in 2000, 40 in 2005 and 181 in 2011. This demontrates that this is a disciplicine with an important scientific impact.

These early research models have focused across all ecosystems (terrestrial, riverscape, seascape) and plant studies comprises 14.5% of the current studies (Storfer et al. 2010). In forest trees, several studies on habitat fragmentation, connectivity or barriers to gene movement and human impact have been carried out to understand how landscape affects the genetic structure of species (Petit et al. 2002, Oddou-Muratorio et al. 2004, Sork and Smouse 2006; Miller et al. 2006; Tollefsrud et al. 2009; Bagnoli et al. 2009), showing accurate information on the status of species genetic resources in a given area, and thus its contribution to the conservation of its diversity. Furthermore, another important advantage is that analysis can be performed at individual level and populations are not necessary to be predefined. The advantage of using individuals as the operational unit are to avoid potential bias in identifying populations in advance and to conduct studies at finer scale (Manel et al. 2003). This is noteworthy, given that, until now, genetic analyses of natural populations have relied on procedures based on the concept that distinct populations of a species exist across a landscape (Miller et al. 2002).

In this context, the characterisation and quantification of both genetic diversity and the mechanisms that influence it require the use of molecular markers that provide a tool for forest genetic conservation (Moritz 1994).

Tools to evaluate genetic diversity

In recent years, microsatellite markers (SSRs) have become the most used markers for studying forest genetics, because they are highly polymorphic, codominant and widespread across the genome (Glaubitz and Moran 2000). From the evolutionary point of view, they are interesting because are present in all species genomes, although distributed in low frequency in coding regions (Tautz and Renz 1984; Powell et al. 1996). These markers are neutral and have proven very useful in studies of genetic diversity, however, are not suitable for estimating adaptive genetic diversity.

Recently, the increased availability of DNA sequences has permitted the development of EST-based SSR markers. ESTs (expressed sequence tag) are expressed in different physiologic conditions of plants. It has been stated that the generation of SSRs from EST is relatively easy and inexpensive because they are sub-products of sequence data from genes or EST that are publicly available. Their main advantages compared with genomic SSRs are that they are quick to obtain and are present in expressed regions of the genome, showing the potential of having known functions (Varshney et al. 2005). Other characteristic is they are more than three times as transferable across species as compared with anonymous SSRs (Peakall et al. 1998; Varshney et al. 2005). Studies based on gene expression hold great potential for shedding light on complex ecological phenomena such as phenotypic plasticity. Such studies can be used to identify candidate genes and to provide a genome wide means of studying the genetic basis of the mechanisms by which organisms respond to environmental changes (Grivet et al. 2008).

Although these techniques can give an adequate view of the situation of the genetic resources in a particular species, the next step to design a strategy for its conservation and sustainable use implies to undertaking other studies focused on the productive organization that is technical and socioeconomic factors. Within the technical aspects to consider are: the forest yield potential (timber and other goods), the products quality, the management practises and the possibility of classifying the product. In the socioeconomic the organization of the sector and the human communities involved in its management should be analysed.

Sweet chestnut: a case of study

Sweet chestnut (*Castanea sativa* Miller), the only species of the genus Castanea in Europe, is one of the multipurpose species of most economic importance in the Mediterranean region. This species has characteristics of interest, not only for fruit and timber but also for its contribution to the landscape and environment, that make it a good model of integration between natural and man driven distribution of biodiversity under changing environmental.

Over many centuries man has influenced the European chestnut populations through propagation and management, leading to a population structure far from one expected in a purely natural situation. For these reasons, chestnut genetic structure is complex (Grossman and Romane 2004). Several situations can be distinguished:

a) High forest. They are chestnut populations that come from seeds (saplings) and each tree has a different genotype. Currently, these stands are dedicated to timber production or simply have an environmental value. Furthermore, in recent times, great attention is paid to trees that stand out from the surrounding vegetation because of their age, size, ecological role and other peculiarities. In general, there is a new acceptance of the importance of ancient woods founded on the recognition of their richness in term of genetic diversity, cultural heritage and historical features (Fay 2002). These trees can reach important diameters, considering as "monumental" those larger than 7 meters in girth at a mean height of 1.30 meters (d.b.h) (Krebs et al. 2005). In this respect, chestnut is a tree of remarkable development and exceptional longevity, and there are examples of chestnut notable for its antiquity and monumentality as "*Cento Cavalli*" from Sicilia (Italia) and "*Castaño Viejo*" from San Román de Sanabria or "*Castaño Santo*" from Istán (Spain).

b) Coppice. They are chestnuts for timber production. In this case, trees come from seeds but regenerate by stump (coppice shoots). In ancient formations, each of these stumps leads to a different set of feet, arranged in circular form. In any case, the resulting formation has a single genotype.

c) Orchards. They are chestnut dedicated to fruit production. Due to the difficulties of the species vegetative reproduction, the clonal varieties are grafted onto seedling rootstocks coming from seeds. In this case, the genetic structure of rootstocks is different to the grafted varieties. Thus, what is expected for rootstocks is that each tree has its own genotype and the grafted part is instead a mixture of clones. The reproduction systems followed in these traditional plantations mean that new rootstocks are the result of the germination of different chestnut varieties (Martín et al. 2009), in which, given the species self-incompatibility (McKay 1942), pollen is from exogenous origin. The fact that fruit production occurs in places with high environmental value and traditional systems, leads to multiple traditional varieties obtained by farmers themselves, a system which tends to maintain a high degree of genetic diversity (Martín et al. 2009, 2010a; Pereira-Lorenzo et al. 2010).

Given these considerations, the improvement in the knowledge of the distribution of the species genetic variability, and its integration in landscape will be a support for management systems that ensure its sustainability, according to the objectives of the strategy described before.

During the last years the consequences of global warming on the shifts in plants phenology, namely in the anticipation of budburst and blooming dates, has been widely discussed (Walther et al. 2002; Jump and Peñuelas 2005). In this respect, the identification of specific loci that underlie divergently selected traits should allow us to address fundamental questions about the genetic basis of population's adaptability to different environmental conditions (Storz 2005). In chestnut, studies aimed at evaluating traits of adaptive significance related to climate change such as water use efficiency, bud burst, bud set and growth, etc., showed a strong population effect for most characters evaluated, indicating differences in adaptation among populations and across the distribution range of the species (Lauteri et al. 1998; Pliura and Erikson 2002; Fernández-López et al. 2005). Furthermore, a study of nine European chestnut populations from areas of contrasting climatic conditions in the

Mediterranean basin, using genomic and genic microsatellite markers, confirmed that combining genomic SSRs and EST-SSRs is a useful tool to give complementary information to explain the genetic and adaptive diversity in chestnut. In this respect, the analysis revealed different clustering pattern between populations, being the grouping according to geographic distances in the case of genomic SSRs and two differentiated groups based on the northern-southern distribution of the populations for genic markers (Martin et al. 2010b). In this later, loci under selection were identified, probably associated with genes controlling phenological traits related to local adaptation at bud burst. The northern populations flushed and formed winter buds later, and grew more than the southern populations, while early flushing could be advantageous for the development of plants before summer drought.

Landscape genetics approach was applied to sixteen populations (high forest), covering the distribution range of the species in Spain, using microsatellite markers. Results revealed a high level of genetic diversity, which in part followed a geographical pattern, but also areas particularly rich in diversity were detected. These results permitted proposing a hypothesis regarding the pattern of genetic structure of the species in Spain, suggesting the influence of both historical climate changes and human activity (Martín et al. in press). Data confirmed the existence of a possible refugium area located in northwest, as described by other authors (Krebs et al. 2004; Fineschi et al. 2000; Mattioni et al. 2008), but also detected a second possible refugium in northeastern Spain. Conversely, the genetic structure of southern populations was the result of man management, given the extensive movement of chestnut genetic material across Europe in the past, and the influence of Romans in the Mediterranean basin (Columela 1979; Adua 1999; Conedera et al. 2004).

This type of studies could provide valuable baseline data that should allow more in-depth studies of landscape genetics associated with other species that can contribute to their conservation and management.

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References

Adua M., 1999. The sweet chestnut throughout history from the Miocene to the third millennium. Acta Hort. 494, 29-36.

Bagnoli F., Vendramin G.G., Buonamici A., Doulis A., Gonzalez-Martinez S., La Porta N. Magri D., Raddi P., Sebastiani F., Fineschi S., 2009. Is Cupressus sempervirens native in Italy? An answer from genetic and palaeobotanical data. Mol. Ecol 18, 2276-2286.

Berrocal del Brío M., Gallardo-Lancho J.F., Cardeñoso-Herrero J.M., 1998. El castaño. Productor de Fruto y Madera. Creador de Paisaje y Protector. Mundi-Prensa. Madrid.

Booy G., Hendricks R.J.J., Smulders M.J.M., van Groenendael J.M., Vosman B., 2000. Genetic diversity and the survival of populations. Plant Biol. 2, 379-395.

CBD (Convention on Biological Diversity), 1992. Río de Janeiro. http: //www.biodiv.org/doc/legal/cbd.

Columela L.J.M. 1979. De Res Rustica. Siglo I d.C. Los doce libros de Agricultura. Editorial Iberia. Barcelona, Spain

FAO, 2001. International Treaty for Plant Genetic Resources for Food and Agriculture. Rome, Italy: Food and Agriculture Organization. ftp://ext-ftp. fao. org/ ag/ cgrfa/ it/ ITPGRe.pdf.

Farina A., 2000. Principles and Methods in Landscape Ecology. Kluwer Academic Press. 236 pp.

Fay N., 2002. Environmental arboricultura, tree ecology and veteran tree management. Arboricultural J. 26, 213-238.

Fernández-López J., Zas R., Díaz R., Aravanopoulos F.A., Alizoti P.G., Botta R., Mellano M.G., Villani F., Cherubini M., Eriksson G., 2005. Geographic variability among extreme European wild chestnut populations. Acta Hort. 693, 181-186

Fineschi S., Taurchini D., Villani F., Vendarmin G.G., 2000. Chlororplast DNA polymorphism reveals little geograpgical structure in Castanea sativa Mill. (Fagaceae) throughout southern European countries. Mol. Ecol. 9, 1495-1503.

Glaubitz J.C., Moran G.F., 2000. Genetic Tools: The use of Biochemical and Molecular Markers, in: Young A., Boshier D., Boyle T. (Eds)., Forest Conservation Genetics. CSIRO Publishing, Australia, pp. 39-52.

Gomez A., Vendramin G.G., Gonzalez-Martinez S., Alia R., 2005. Genetic diversity and differentiation of two Mediterranean pines (Pinus halepensis Mill. and Pinus pinaster Ait.) along a latitudinal cline using chloroplast microsatellite markers. Drivers Dist. 11, 257-263.

Grivet D., Sork V.L., Westfall R.D., Daviss F.W., 2008. Conserving the evolutionary potential of California valley oak (Quercus lobata Née): a multivariate genetic approach to conserving planning. Mol. Ecol. 17, 139-156.

Holderegger R., Wagner H.H., 2008. Landscape Genetics. BioScience 58,199-207.

Holderegger R., Buehler D., Gugerli F., Manel S., 2010. Landscape genetics of plants. Trends Plant Sci. 15, 675-682.

Jump A.S., Peñuelas J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecol. Letter 8, 1010-1020.

Kozak K.H., Graham C.H., Wiens J.J., 2008. Integrating GIS-based environmental data into evolutionary biology. Trends Ecol. Evol. 23, 141-148.

Krebs P., Conedera M., Pradella M., Torriani D., Felber M., Tinner W., 2004. Quaternary refugia of the sweet chestnut (Castanea sativa Miller): an extended palynological approach. Veg. Hist. Archaebot. 13, 145-160.

Krebs P., Conedera M., Fonti P., 2005. The inventory of the giant chestnut trees in the southern Switzerland. Acta Horticulturae 693, 171-178.

Latta R.G., 2006. Integrating patterns across multiple genetic markers to infer spatial process. Landscape Ecol. 21, 809-820.

Lauteri M., Monteverdi M.C., Sansotta A., Cherubini M., Spaccino L., Villani F., Küçük M., 1998. Adaptation to drought in European chestnut. Evidences from a hybrid zone and from controlled crosses between drought and wet adpated populations. Acta Hort. 494, 345-353.

Mace G.M., Gittleman J.L., Purvis A., 2003. Preserving the tree of life. Science 300, 1707-1709.

Manel S., Schwartz M.K., Luikart G., Taberlet P., 2003. Landscape genetics: combining landscape ecology and population genetics. Trends Ecol. Evol. 18, 189-197.

Martín M.A., Alvarez J.B., Mattioni C., Cherubini M., Villani F., Martín L.M., 2009. Identification and characterisation of traditional chestnut varieties of southern Spain using morphological and simple sequence repeats SSR markers. Ann. Appl. Biol. 154, 389-398.

Martín M.A., Mattioni C., Cherubini M., Taurchini D., Villani F., 2010a. Genetic characterisation of traditional chestnut varieties in Italy using microsatellite (SSRs) markers. Ann. Appl. Biol. 157, 27-44.

Martín M.A., Mattioni C., Cherubini M., Taurchini D., Villani F., 2010b. Neutral and adaptive genetic diversity in European chestnut populations by means of genomic and genic microsatellite markers. Tree Genet. Genom. 6, 735-744.

Martín M.A., Mattioni C., Molina J.R., Álvarez J.B., Cherubini M., Herrera M.A., Villani F., Martín L.M., Landscape genetic structure of chestnut (Castanea sativa Mill.) in Spain. Tree Genet. Genom. in press. DOI: 10.1007/s11295-011-0427-x.

Mattioni C., Cherubini M., Micheli E., Villani F., Bucci G., 2008. Role of domestication in shaping Castanea sativa genetic variation in Europe. Tree Genet. Genom. 4, 563-574.

McKay J.W., 1942. Self-sterility in the Chinese chestnut (Castanea mollisima). Proc. Am. Soc. Hort. Sc. 41, 156-16.

Miller M.P., Blinn D.W., Keim P., 2002. Correlations between observed dispersal capabilities and patterns of genetic differentiation in four aquatic insect species from the Arizona White Mountains, USA. Freshwater Biol. 47, 1660–1673.

Miller M.P., Bellinger M.R., Forsman E.D., Haig S.M., 2006. Effects of historical climate change, habitat connectivity, and vicariance on genetic structure and diversity across the range of the red tree vole (Phenacomys longicaudus) in the Pacific Northwestern United States. Mol. Ecol. 15, 145-159.

MIMAM, 2006. Estrategia de Conservación y Uso Sostenible de los Recursos Genéticos Forestales. Madrid, Spain.

Moritz C., 1994. Application of mitochondrial DNA analysis in conservation: a critical review. Mol. Ecol. 3, 401-411.

Namkoong G., 2001. Forest Genetics: pattern and complexity. Can. J. Forest Res. 31, 623-632.

Namkoong G., Ouédrago A.S., 1997. Developing decision making support strategies for conservation and sustainable use of forest genetic resources. Research proposal, IPGRI-UBC, IPGRI. Rome, Italy.

Oddou-Muratorio S., Demuse-Munsh B., Pélissier R., Gouyon P.H., 2004. Impacts of gene flow and logging history on the local genetic structure of scattered tree species, Sorbus torminalis L. Crantz. Mol. Ecol. 13, 3689-3702.

Palmerg-Lerche C., 1999. Conservation and management of forest genetic resources. J. For. Sci. 11, 286-302.

Pautasso M., 2009. Geographical genetics and the conservation of forest trees. Perspect. Plant Ecol. 11, 157-189.

Peakall R., Gilmore S., Keys W., Morgante M., Rafalski A., 1998. Cross-species amplification of soybean (Glycine max) simple sequence repeats (SSRs) within the genus and other legume genera: Implications for the transferability of SSRs in plants. Mol. Biol. Evol. 15, 1275-1287.

Pereira-Lorenzo S., Costa R., Ramos-Cabrer A., Ribeiro C., da Silva M., Manzano G., Barreneche T., 2010. Variation in grafted european chestnut and hybrids microsatellite reveals two main origins in the Iberian Peninsula. Tree Genet. Genom. 5, 701-715.

Petit R.J., Latouche-Hallé C., Pemonge M.H., Kremer A., 2002. Chloroplast DNA variation of oaks in France and the influence of forest fragmentation on genetic diversity. Forest Ecol. Manag. 156, 115-129.

Pliura A., Eriksson G., 2002. Genetic variation in juvenile height and biomass of open-pollinated families of six Castanea sativa Miller populations in a 2X2 factorial temperature x watering experiment. Silv. Genet. 51, 152-160.

Poffenberger M., 1996. Communities and forest management. IUCN. Cambridge, UK.

Powell W., Machray G.C., Provan J., 1996. Polymorphism revealed by simple sequence repeats. Trends Plant. Sci. 1, 215-222.

Shachak M., Boeken B., Groner E., Kadmon R., Lubin Y., Meron E., Neeman G., Perevolotsky A., Shkedy Y., Ungar E.D., 2008. Woody species as landscape modulators and their effect on biodiversity patterns. Bioscience 58, 209–221.

Sork V.L., Smouse P.E., 2006. Genetic analysis of landscape connectivity in tree populations. Landscape Ecol. 21, 821-836.

Storfer A., Murphy M.A., Evans J.S., Goldberg C.S., Robinson S., Spear S.F., Dezzani R., Delmelle E., Vierling L., Waits L.P., 2007. Putting the ‘landscape’ in landscape genetics. Heredity 98, 128-142.

Storfer A., Murphy M.A., Spear S.F., Holderegger R., Waits L.P., 2010. Landscape genetics: where are we now? Mol. Ecol. 19, 3496–3514.

Storz J.F., 2005. Using genome scans of DNA polymorphism to infer adaptive population divergence. Mol. Ecol. 14, 671-688.

Tautz D., Renz M., 1984. Simple sequences are ubiquitous repetitive components of eukaryotic genomes. Nucleic Acids Res. 12, 4127-4138.

Tollefsrud M.M., Sønstebø J.H., Brochmann C., Johnsen Ø., Skrøppa T., Vendramin G.G., 2009. Combined analysis of nuclear and mitochondrial markers provide new insights into the genetic structure of North European Picea abies. Heredity 102, 549-562.

Turner M.G., 1989. Landscape Ecology: The Effect of Pattern on Process. Ann. Rev. Ecol. Syst. 20, 171-197.

Varshney R.K., Graner A., Sorrells M.E., 2005. Genic microsatellite markers in plants: features and applications. Trends Biotechnol. 23, 48-55.

Walther G., Post E., Convey P., Menzel A., Parmesank C., Beebee T.J.C., Fromentin J.M., Hoegh-Guldberg O., Bairlein F., 2002. Ecological responses to recent climate change. Nature 416, 389-395.

Wilson E.O., 1988. Biodiversity. National Academy Press. Washington, DC.

World Commission on Environment and Development, 1987. Our common future Oxford University Press. Oxford, UK.

Wright J.P., Jones C.G., 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56, 203–209.

Wulder M., Hall R., Coops N., Franklin S., 2004. Remotely sensed data for ecosystem characterization. BioScience 54, 511–521.

Young A., Boshier D., Boyle J., 2000. Forest Conservation Genetics: principles and practice CSIRO- CABI Publishing. New York.