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Olevi Kull's lifetime contribution to ecology

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Olevi Kull during a visit to a forest ecology station in French Guyana, January 2006 (Photo: Meelis Pärtel).

> *Heavenly tune which none can hear*
> *Of human mould with gross unpurged ear*
> Milton (Arcades)

Summary In this article dedicated to Olevi Kull (June 22, 1955–January 31, 2007), we draw on his writings (in English and translated) to outline his thoughts on the relationship between scientists and science. We provide a brief synthesis of his most important work, give a short account of his career and, to bring the man into focus, share some personal stories of interactions with him. Kull considered that for a personal understanding to become scientific knowledge it must be explained convincingly based on theory and empirical support, and then taught to others in both spoken and written words. He saw the last step as the main distinction between learning and science. Olevi Kull's approach to science relied on two principles: first, linking theory and experiments in challenging settings, e.g., to test the generality of his ideas he often challenged them in multi-layered, mixed-species canopies. Second, he insisted on setting experiments to test assumptions used in quantitative analyses or in explaining an observed outcome; this, at times, led to falsification of commonly held ideas, thus enhancing ecophysiological understanding. After describing Kull's application of these principles, we give a brief synthesis of his most important work, in which he demonstrated through experimentation and modeling how the vertical distribution of leaves in canopies is consistent with the acclimation of the photosynthetic apparatus. We also review some of his findings on the interactive effects of carbon dioxide and ozone on canopy photosynthesis.

Keywords: chlorophyll:nitrogen ratio, light, $O_3 \times CO_2$ interaction, photosynthetic modeling.

Olevi Kull's views on the source and communication of ideas

To understand how a system works, the system's components must be defined and its behavior elucidated. For this personal understanding to become scientific knowledge, it must be explained convincingly, through logical arguments, descriptions, calculations, measurements and experiments, both theoretically and empirically. Then, the personal understanding should be taught to others, in both spoken and written words, in ways conducive to learning. Thus, *my* knowing (*teadmine*, in Estonian) becomes *our* knowledge (*teadus* = science; Kull 2007). Those who knew Kull would remember how emphatic he was about the essential role that teaching new ideas plays in science.

Discussing science in his final published article he states (Kull 2007):

> … generating ideas and explaining phenomena is a rather small and certainly not the main part of a scientist's work. The process of obtaining new knowledge that a scientist experiences in his empirical or theoretical activities does not differ in any way from studying. It only becomes science when other people, especially other scientists, accept the new knowledge as a part of the collective scientific knowledge. For this one has to convince others. Convince that the knowledge is new, that it is reasonable, that it fits with prior knowledge, that it allows explaining phenomena that have not been explained before … For convincing, one must use the same language, definitions and symbols used by those to be convinced. The activity of convincing others is the most important part in scientists' work …

To relate to Kull's focus on precise definitions of systems and their components, the understanding of their behavior and the need to communicate effectively, one must relate to his experiences under two scientific cultures that differ greatly in their rules of argument. Kull regularly discussed the plurality of "scientific cultures," of which the Soviet–Western dichotomy is but one example relevant to his scientific work. He began his career conducting research within the Soviet scientific culture, and moved fairly early to operating under the rules of the Western scientific method. On this he writes:

> Scientific knowledge is a part of the collective knowledge of a group of people, and its boundaries are not clear. Whether new knowing is deemed part of the collective knowledge is largely consensual, and this consensus is carried forth by scientists. Also largely consensual are the ways of presenting one's results, which methods and analyses are acceptable and which are not, and what kinds of arguments can be used in deductive reasoning. What is most important, however, is that the range of important problems is also consensual. Although one cannot say that the Russian-speaking science world was completely isolated from the English-speaking one, the barrier between them was sufficient for these fundamental consensual aspects to be shifted in relation to one another. So the understanding in the Russian-speaking world of science differed greatly in what makes a good research paper, how to execute a convincing research experiment, and also (at least in part) what are the essential questions needing to be addressed (Kull 2007).

And so, when discussing his own research achievements while using the non-western approach, he would describe interesting scientific results; yet he would not translate the articles (written for instance in Russian or Estonian) because he believed they should be taken only in the context of the rules under which the research was conducted. This position had little to do with the quality of the science. For example, one of the central arguments in his Russian-language dissertation, originating from investigation of respiration of trees, was that on a certain timescale, plant respiration is proportional to photosynthetic productivity (Kull 1987, Kull and Kull 1989). This understanding was based on two insights. First, that the maintenance respiration is mainly attributable to the turnover of large enzymes and other pools of organic compounds, rather than to low-level processes such as those required to maintain cellular gradients. Turnover processes may use larger quantities of assimilates and depend on the size of photosynthate pool in the plant. Second, that the proportionality between photosynthesis and maintenance respiration can be shown only when photosynthesis is integrated over a period long enough to affect the size of the photosynthate pool of a plant as a whole, which in trees may require extended periods of continuous measurements. This was rarely done, perhaps resulting in the more commonly observed relationship between maintenance respiration and biomass (Thornley 1970). Kull's insights de-emphasized biomass as the sole driver of maintenance respiration, which was the broadly held view at the time. Later, when process-level partitioning of respiration was further elucidated (as summarized by Thornley and Cannell 2000, Cannell and Thornley 2000, Amthor 2000), the western literature has seen this view expressed more frequently.

Main foci of Olevi Kull's research and key findings

Kull's key contribution to science has been the description and interpretation of mechanisms and rules that govern the acclimation of the photosynthetic machinery to the large vertical gradient of illumination present in dense plant canopies. His research included assessment of the changing relative quantities of light-absorbing and carbon-fixing components of the machinery, the relationships between the nitrogen and carbon cycles, and the modeling of production processes in relation to plant community structure. He also investigated the joint effects of elevated concentrations of ozone and carbon dioxide on photosynthesis. In this section, we describe Kull's approach to science and his accomplishments, acknowledging that he would be first to insist that his contribution is the product of close collaboration with his teachers, students and colleagues.

Kull's approach to science relied on two principles, the first of which was linking theory and experiment in challenging settings. In some settings, he used trees of a single species in a natural canopy growing along a light gradient (Kull and Niinemets 1993) and compared the results with open-grown trees as reference (Kull and Koppel 1987), or of two species from the same genus, comparing their behavior under native soil conditions or perturbed by fertilization (Kull et al. 1998, Merilo et al. 2006). However, his signature approach was to test ideas on several co-occurring species sharing the canopy volume that exhibit some similar and some distinguishing characteristics (Kull and Niinemets 1993, Kull et al. 1995). This multi-species approach tested the generality of conclusions, permitted honing of theory, and set the stage for follow-up investigations. A second principle was to devise experiments to test assumptions used in quantitative analyses or to explain phenomena observed in previous studies. At times, this led to discarding an assumption made during an earlier experiment (Laisk et al. 1989) and replacing it with a more profound understanding of ecophysiological function (Kull and Moldau 1994). We briefly demonstrate each approach in the following sections.

Acclimation of photosynthetic machinery to the vertical gradient of light in the canopy

Optimality models are common in biology. Yet, the underlying assumptions of such models are often not clearly analyzed. After reading Robert Rosen's (1967) book, Kull wrote about the optimality principle in biology in a review during his candidacy exams (Kull 1983):

> … in many instances where biological processes are modeled using the optimality principle, it is very difficult to demonstrate the connection between the local optimum and the mechanism of natural selection. This is for two reasons. First, … parameterizing the directional function (that is optimized in the evolutionary process) for more complex objects is very difficult, and second, some of the optimizable processes in biological systems may derive directly from purely physical principles.

Kull expressed his thoughts on optimality models in several articles. For example:

> Most acclimation models based on optimality do not consider the fact that redistribution of photosynthetic machinery in canopies according to local environmental conditions is clearly a plant-level phenomenon, which depends on plant-internal resources, particularly the amount of nitrogen and sugars. Experimental data show that the distribution of photosynthetic machinery in the crown depends directly on plant species, as well as the position of the plant in the community's canopy. Furthermore, optimality-based models (if they become capable of adequately describing reality) do not include a description of the mechanisms responsible for the redistribution of photosynthetic capacity among leaves (Kull and Niinemets 2000).

In an elegant sequence of experimental and modeling studies, beginning with distinguishing the characteristics of light- and shade-demanding species, followed by a search for the mechanistic underpinnings of the photosynthetic light response (in relation to nitrogen and chlorophyll), and culminating with a comprehensive theoretical synthesis, Kull provided the principal ideas and tools for quantifying photosynthesis down the canopy of a multi-species forest. This work on light distribution, the biochemical and structural properties of leaves, and nitrogen uptake and allocation (Kull and Niinemets 1993, 1998, Kull et al. 1995, 1999, Kull and Aan 1997, Kull and Tulva 2002, Meir et al. 2002, Eichelmann et al. 2005, Laisk et al. 2005) led to a synthesis of basic principles in a manner consistent with the vertical distribution of light, nitrogen and photosynthetic capacity in canopies (Kull and Jarvis 1995, Kull and Kruijt 1998, 1999, Kull and Tulva 2002, Aan et al. 2006). In essence, resources for light capture and for the processing of the captured energy (photosynthesis) are expected to be shared strictly reciprocally: less for light capture and more for photosynthesis in upper layers and vice versa in the lower layers. Although other researchers at that time were asking similar questions on the relationship between light and nitrogen (e.g., Hirose and Werger 1987, 1994), the novelty and thoroughness of Kull's work led to an invitation for a review of models of photosynthetic acclimation in canopies, where he discussed the limitations of current models and ideas on how to overcome these limitations (Kull 2002).

Where the objective is to scale photosynthesis from leaves to the canopy of a plant community using the least amount of physiological information, he concluded that the parameters related to nitrogen-dependence of light utilization may serve best (Kull and Jarvis 1995). Later work elaborated on the approach. Kull (2002) suggested that nitrogen concentration, nitrogen use and chlorophyll:nitrogen ratio are the most important parameters in the busy parameter space accompanying light-dependent changes in photosynthesis. Most studies concentrate on either chlorophyll or nitrogen concentration. Leaf chlorophyll represents the capacity of the surface to absorb light, whereas nitrogen concentration is related to photosynthetic capacity. The ratio of chlorophyll to nitrogen is therefore a convenient measure of the balance between the light-harvesting and biochemical components of the photosynthetic machinery, vital to the acclimation of leaves to the prevailing light conditions (Kull and Niinemets 1998). Quantifying both variables simultaneously was almost unique to Kull's group, leading to analysis of the relationship between chlorophyll and nitrogen, and ultimately to using this ratio in modeling photosynthesis.

The quantitative basis for Kull's approach to the later scaling has been presented in two, as yet underappreciated articles (Kull and Kruijt 1998, 1999). This modeling scheme is Kull's most novel contribution, and we anticipate that some variant of this model will ultimately be routinely incorporated into photosynthetic models that preserve a realistic characterization of canopy structure for estimating the distribution of light in the canopy. An adaptation of the approach may be facilitated by the increasing capability to extract information on both chlorophyll and nitrogen concentrations from remotely sensed data (Asner and Vitousek 2005, Zhang et al. 2005, 2006). The approach is particularly useful, because it can be applied to estimate photosynthesis within the crown of an individual tree, as well as to a canopy composed either of several species sharing a single horizontal layer or stratified into several layers. The model predicts that fast-growing communities will have a less optimal photosynthetic distribution than slow-growing communities. This has implications for the way remotely sensed data (e.g., MODIS-based APAR estimates) should be used to scale canopy photosynthesis and gross primary production.

On the comprehensive approach to studying processes at the ecosystem level, Kull wrote (Kull and Niinemets 2000):

> The physiology of photosynthesis is relatively well studied, particularly at the leaf level. Serious problems appear when trying to estimate the cumulative photosynthesis of a canopy or plant community. But it is this that we need in order to understand the dynamics of net CO_2 flux. Physiologists generally study relatively fast processes. To understand the behavior of the canopy, one has to know not only the leaf-level physiology but also the constraints (boundary conditions) and processes that determine the distribution of photosynthetic machinery in canopy … Due to large environmental gradients in the canopy the photosynthetic machinery acclimates, leading to a very uneven distribution of leaf photosynthetic capacity. In order to calculate the canopy photosynthesis and forecast changes in response to environmental conditions, one must know the mechanisms behind the acclimation.

Kull noticed that the vertical distribution of leaf area, quantitatively describing the community, is often, yet not always, arranged into layers (Kull et al. 1995, Kull and Niinemets 1998, Kull 2002), and demonstrated the need to consider nitrogen use in explaining the distribution of photosynthesis down the canopy. A comprehensive analysis of an ecosystem-level process requires that the net balance of elemental cycling is quantified; this, in turn, necessitates a simultaneous consideration of processes at multiple temporal and spatial scales. Thus, analyzing the behavior of individual organisms in the context of the whole ecosystem can result in understanding of both the balance among its constituents and the role of acclimation in achieving this balance. The balance and capacity to adapt are reflected in the aggregated behavior and would permit prediction of the net ecosystem response to perturbations.

The quote from Milton's Arcade, at the head of this article, has been used to describe the difficulty in quantifying the temporal dynamics of growth resources (Oren and Schulze 1989). In that study, it was recognized that plant requirements for one nutrient change relative to others over seasons and years, depending on phenology, weather and the stage of stand development. Thus, instead of a balanced demand for nutrients that is characterized by a single quantity of each element relative to another (e.g., Ingestad 1979), for a plant to be free of limitation by any nutrient at any time the supply of nutrients must reflect a balance that is shifting over time (Linder and Rook 1984). Acidic precipitation disrupts that dynamic balance, thus producing a *nutritional disharmony*, ultimately leading to decline.

Kull's modeling of photosynthesis within mixed-species canopies similarly accounts for dynamics that depend on resources provided by the soil and the atmosphere, and are affected by the plant's own structure and carbohydrate management. He writes (Kull 2002):

> … [the] acclimation of the amount of photosynthetic apparatus occurs due to permanent turnover of this apparatus, and, because the equilibrium amount of this apparatus depends on resource availability, primarily nitrogen and carbohydrates.

For the community of tree physiologists to recognize the elegance of the approach presented by Kull and Kruijt (1998, 1999) and hear the harmony in its composition, more ears would have to be tuned to this concept. Remembering his thoughts about scientific knowledge, Kull simply did not have enough time to convince enough researchers to test the turnover models more completely, and to elucidate "[the] mechanism responsible for changes in the relative share of light-harvesting apparatus …" (Kull 2002). His articles specify several interesting challenges for the community.

Other major research thrusts

The introductory web page of his Chair states:

> The work done at the Chair of Eco-physiology involves mainly three fields: 'classical' plant eco-physiology, carbon cycling in forest ecosystems and the effect of global climate change on the vegetation.

To those who knew him, it was clear that Kull was most excited when discussing research concerning vertical canopy structure, and the concomitant gradients in nitrogen and photosynthesis. However, he considered it imperative that Estonian science be closely interfaced with that of countries with advanced research and thus pursued several additional research topics that facilitated such international collaboration.

Effects of ozone on the photosynthetic machinery Kull conducted a series of experiments to study the effects of ozone and elevated carbon dioxide concentration ($[CO_2]$) on plants. Among the first important results, obtained in collaboration with the working group of Agu Laisk, was that ozone concentration inside a leaf is zero (i.e., ozone is rapidly absorbed into or reacts on the cell surface; Laisk et al. 1989). Subsequent experiments serve as examples of the drive to test assumptions made in one experiment, leading to discoveries in the next. Two experiments demonstrated that the sensitivity of photosynthetic parameters to ozone differed between soil- and sand-grown plants; the first experiment eliminated differences in ozone uptake rate and attributed the differential sensitivity to unequal chemical capacity for scavenging in the cells (Moldau et al. 1991); the second eliminated an alternative explanation, stomatal patchiness, as the cause of the differential sensitivity (Moldau and Kull 1993). In a final article in this series, the assumption that leaf surface conductance to ozone can be neglected was discarded, by demonstrating the importance of cuticular conductance to the interpretation of results, especially from short-term experiments in which leaves were exposed to low ozone concentrations (Kull and Moldau 1994).

Later, Kull and colleagues showed that the effects of ozone and elevated $[CO_2]$ are not additive, and that elevated $[CO_2]$ may amplify the effect of ozone (Kull et al. 1996). The predominant theory at the time was that elevated $[CO_2]$ ameliorates to some extent the detrimental effects of ozone on photosynthesis (Allen 1990). In one of the first experiments to quantify the response of tree species to simultaneous exposure to high concentration of both O_2 and O_3, Kull et al. (1996) disproved the generality of the compensation theory. They found that the interactive effect was more negative than the effect of O_3 alone, and proposed a plausible mechanism for the observed response. The ozone sensitivity of different species seems to be related to their photosynthetic capacity, nitrogen uptake, light response and secondary defense compounds (Kull et al. 1996). However, the mechanisms of the interactive effects of elevated [CO_2] and [O_3] are yet to be conclusively elucidated. The hypotheses proposed served to generate new studies, some of which are taking place in free-air $CO_2 \times O_3$ experiments in the USA, one in Wisconsin and another in Illinois. Although elevated [CO_2] may not ameliorate the effect of ozone on photosynthesis, Kull et al. (2003, 2005) demonstrated, based on empirical evidence and model-based results from the Aspen FACE (in Wisconsin), that elevated [CO_2] can ameliorate the effect of ozone by affecting the amount and distribution of leaf area in the canopy.

Environmental effect on forest carbon balance Early investigations combining both empirical observations and modeling of respiration and photosynthesis of spruce (Kull et al. 1985, Kull and Koppel 1987), contributed to studies on gradients of photosynthesis in the canopies of plant communities and to studies on forest carbon balance. The latter, including investigation of the effects of forest harvesting on the carbon budget of forest ecosystems, were complemented by studies of carbon cycling via measurements of carbon pools in different ecosystem compartments (Kull and Szava-Kovats 2003). Carbon stocks of soil, litter and coarse woody debris were measured in a chronosequence of forest stands, and modeled based on measured fluxes of litter fall and soil respiration. The studies attempt to quantify the link between carbon and nitrogen cycling, including the degree to which perturbations of the carbon cycle are reflected in the nitrogen cycle. Forthcoming results from these studies are likely to contribute to basic understanding of ecosystem processes, biosphere–atmosphere exchanges of carbon, and forest management strategy for mitigating the rate of increase in atmospheric [CO_2].

A brief biography

Olevi Kull was a leader of Estonian ecology and an eminent scholar in forest ecology and physiology. He (and his brother, Kalevi) developed an interest in science at a young age, in part thanks to their parents—Lembit and Hilja Kull, both applied mathematicians. Olevi devoted 35 years of his brief life to ecology.

While in high school, Olevi participated in ecological field work, joining the summer expedition of Juhan Ross's group (along with Vello Ross, Tiit Nilson and others). In his first two undergraduate years at Tartu University, he studied physics, laying the foundation for the quantitative rigor he later brought to his research. He ultimately majored in forest management at the Estonian Agricultural Academy. During much of that time, he worked in August Örd's group at the Nature Conservation Laboratory of the Estonian Forest Institute. His diploma dissertation was highly praised and won several awards. Joining Toomas Frey's Plant Ecology Group in the Systems Ecology Section of the Institute of Zoology and Botany, he was given the responsibility of establishing a program for measuring gas exchange in trees. Combining his strong background in physics with exceptional technical aptitude, he became an expert in constructing gas exchange measurement systems and other biophysical instruments. His work at that time began to focus on the respiratory processes in trees. Olevi, and Kalevi, defended their doctoral dissertations in 1987 (on their mother's birthday), both produced under Toomas Frey's supervision at Tartu University. Their closely related dissertations led to a monograph on the dynamic modeling of tree growth (Kull and Kull 1989).

Olevi became Head of the Tartu branch of the Estonian Institute of Ecology in 1990. In 1999, he was elected Tartu University professor in applied ecology, and thus the leader of the Chair of Ecophysiology of Tartu University's Institute of Botany and Ecology. In 2002, the Estonian Ministry of Education and Research established The Center for Theoretical and Applied Ecology, directed by Olevi, as one of ten Centers of Excellence. In that capacity he also led the affiliated Graduate School of Ecology and Environmental Sciences. In 2004, Olevi was selected Head of the Institute of Botany and Ecology at Tartu University.

Despite mounting administrative pressures, Olevi remained engaged in science. He organized several high-profile international conferences, including the IUFRO Canopy Processes meeting on *Canopy Dynamics and Forest Management: A Missing Link* (Linder et al. 2001), and the joint event by the Nordic Network for Carbon Dynamics in Managed Terrestrial Ecosystems and the Graduate School of Ecology and Environmental Sciences in 2006 on *Tree Canopy—Structure and Functioning—From Below and Above* (the best meeting in which Oren has ever participated). The final major project established by Olevi, again drawing on his technical capabilities, is a study of the potential responses of forests to changes in humidity under otherwise unaltered conditions. To accomplish this, Olevi helped design a free-air humidity experiment, just commencing at Järvselja Experiment Station. In all, Olevi published 60 papers in English, 9 in Russian and 13 in Estonian; he received the Wilhelm Leopold Pfeil Award (Freiburg Breisgaus, Germany, in 1990), and twice the laureate of Estonian Science Award (in 1995, as a member of the Institute of Ecology, and in 2000, for his work on *Acclimation of Photosynthesis in the Plant Canopy* with Ü. Niinemets).

Olevi had a clear sense of the history of science in Estonia, not only how research must be viewed in the context of the prevailing scientific culture, but also how certain individuals with a particular background can have a long-term effect on the development of a scientific field. In his final published article (Kull 2007), Olevi describes some general aspects of the field to which he belonged—the Estonian school of vegetation biophysics, founded largely by Juhan Ross. This school was born in the 1960s, and flourished in the 1970s when Olevi began his life in science, and continues today, primarily through the work of Agu Laisk, and the research groups of his and Olevi's students. The characteristic feature of this school, which has influenced many Estonian (and non-Estonian) scientists, is a strong theoretical foundation, the skill of mathematical modeling linked to well-designed experimental work (including building their own instruments and thorough understanding of the principles of their operation). He writes:

> Our field of work has a strong and long-standing tradition in Estonia. First, we want to emphasize the significance of Juhan Ross and his students and coworkers. Although he was a physicist, it is because of his influence that ecology research in Estonia is characterized by the approach usually associated with hard sciences. The works of Juhan Ross and his students also had a strong influence on the development of Toomas Frey's ecosystems group. It is that group from which we emerged (Kull and Niinemets 2000).

The Systems Ecology Section of the Institute of Zoology and Botany, where Olevi worked in the early 1980s, was one of the major centers in Estonia advancing ecological and sustainability views. The influence of these views surfaced later, when Olevi wrote (Kull and Niinemets 2000):

> … it is becoming clearer than ever that the number of people and the industrial power they command are sufficient to trigger irreversible changes in the global environment.

Thus, as the Director of the Center of Excellence in Basic and Applied Ecology, Olevi focused the mission of the Center on developing "... applications that support sustainable development and conservation of natural resources in Estonia." (Kull 2004)

Concluding sentiments

Oren was fortunate enough to spend an occasional private evening with Olevi. It began when we both were just beginning scientists in the mid-1980s and ended at the course on canopy processes that Olevi organized just weeks before his passing. We shared wine, blocked outside clatter and talked about life and science. At some moment during most of these occasions, he would lean towards me and slowly, almost painfully ask a question, clearly on a scientific issue that had occupied his thoughts for quite some time. For some reason, I always had the impression that he expected me to come up with a better answer than he had thought out. I rarely did. "What do you see when you look at a leaf?" he asked me once, nearly twenty years ago. After listening for a short while to my technical and rather standard answer, he interposed "I think we best view it as a parcel of ocean kept alive in a dry atmosphere." I can almost hear him saying it as I write. It rekindled my interest in plant water relations and provided me with an engaging sentence to begin my classes on plant ecology.

About a year ago, Olevi gave me an album of music he liked very much, "Oota" ("Wait") by the group Jääär (Ice Verge). Among the songs, one describes quite well how many who knew him feel:

Simple Things *(Lihtsad asjad)*
You are used to swim
in life's even flow
feeling all you need is yours for ever
You do not see
the shivery around you
where your small warm world comes together

Simple things come easy
you notice their value
when they're gone
and you are wanting
Plain men and women
to know their value
you must be alone
without them

Tomorrow better than yesterday
a day in your hands like water
flowing through fingers and gone
look around you
and notice the trifle
it is worth more than you believe

Indeed. But there is also radiance in the recognition that Olevi's life in ecology was true to his philosophy of what makes science. As Kalevi wrote about his brother (translated from Estonian):

> To notice problems, have the skill to word questions, devise a clear plan for finding the answers, and thereby reach understanding of the deeper mechanisms of life. Like Olevi. This way it is wonderful to be a scientist (K. Kull 2007).

Olevi's friends and colleagues, worldwide, are helping to ensure that this radiance continues by helping to expose Estonian graduate students to international experience and training (see http://www.ut.ee/sihtasutus/index.php?lk=13&stipendium=61).

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