THE KELO TREE, A VANISHING SUBSTRATE OF SPECIFIED WOOD-INHABITING FUNGI

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Abstract: In natural circumstances very old pine trees (*Pinus sylvestris* L.) usually die while still standing. At the time of their death the trees have reached up to 300–500 years of age, and while dead they may still stand for another 200–500 years or even more. Such long-ago died, debarked, standing pines are called in Finnish the 'kelo', and the term is here proposed for common usage. When the kelo trees finally fall down, they make up a niche for a number of highly specialized fungi. A list is given on typical such Basidiomycetes (polypores and corticiaceous fungi). The onset of forest cutting virtually eradicated that kind of substrate from Central European lowland forests, as well as from the Mediterranean, which resulted in large-scale disappearance of many specialized fungi. Due to the slow development and extremely slow rate of decay of the kelo trees, also the fungi living on them seem to be slow in their colonization, needing a continuity in the supply of the substrate. Therefore scarce and random occurrence of dead standing pines will not suffice for the survival of fungi specialized to live on the kelo.

Key words: Basidiomycetes, fungi, kelo, old-growth forest, *Pinus sylvestris*

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INTRODUCTION

Large-scale cutting of forests has lasted in Central Europe for about two millennia, and in the Mediterranean longer still. According to Pliny (Gaius Plinius Secundus, AD 23–79), when the Roman army penetrated Hercynia (the present-time mid Germany), soldiers made more effort pushing their way through the primeval forests with giant oak, beech, elm and pine, than fighting against locals. All the present virgin forest reserves in, e.g., Germany, have in fact been cut down many times in the past. A glimpse in the original Central European lowland forest can best be seen in Białowieża of eastern Poland.

The Białowieża forest has some characteristics unusual for other forest reserves of the area, having the same vegetation type. Giant, dead, decorticated, silver-grey pine trees stand here and there. A mycologist may be surprised to see, for instance, that in this rich lowland forest *Fomitopsis rosea* (Alb. & Schwein.: Fr.) P. Karst. is much commoner than *F. pinicola* (Sw.: Fr.) P. Karst. on fallen spruce trees. Some great rarities are frequently seen, for instance *Pycnoporellus alboluteus* (Ellis & Everh.) Kotl. & Pouzar*, Antrodia crassa* (P. Karst.) Ryvarden*, Dichomitus albidofuscus* (Domański) Domański, *Rigidoporus crocatus* (Pat.) Ryvarden and *Antrodiella foliaceodentata* (Nikol.) Gilb. & Ryvarden. The sheer number of wood-inhabiting species is much higher there than in other corresponding protected areas. Why is that?

Fungi living in the oldest virgin forests have many characteristics and demands that cannot be met under human interference. One is the need of high volume of coarse woody debris (CWD), i.e. fallen trunks, natural stumps, big fallen branches etc. Sippola *et al.* (1998), Siitonen *et al.* (2000, 2001) and Siitonen (2001) have discussed the amounts of CWD in old-growth forests and its ecological importance there. Another is the conti-

nuity: freshly fallen trunks should be available continuously within the reach of fungal populations, and such circumstances should have lasted uninterrupted for decades, centuries and even millennia. This never-ending supply of fallen trunks is important because certain fungi usually occupy trunks of only a certain decay stage and certain diameter; Renvall (1995) illustrated this thoroughly in an example from Lapland. Once this continuum is broken by clear cutting, selective logging (Sippola *et al.* 2001), or gathering of fallen trunks from the forest, return to original state is very slow, and if the disturbance is large-scale, the disappearance of many sensitive fungi may be irreversible. For this reason species-rich old-growth forests cannot be reclaimed by just letting the trees grow old.

Two processes of regeneration occur side-by-side in natural forests: primary succession after large-scale destruction in wildfires, and regeneration via gap dynamics in areas that have avoided burn (fire refugia); in the latter the forest renews in a mosaic-like fashion, as single old trees or groups of trees randomly fall down and give space to a new generation (Kuuluvainen 1994). Because of this, the architecture of old-growth forest is less uniform than in managed forests, and there are much more microhabitats available. In particular the presence of very old tree individuals among the younger ones is an important source of voluminous substrates after their fall-down. In the past natural forests underwent extensive forest fires ignited by lightning or man (Niklasson & Granström 2000; Pitkänen & Grönlund 2001). However, nowadays for instance in the Nordic countries forest fires are so effectively controlled and extinguished that charred wood, important substrate for some species, has virtually disappeared. Such fire-depending polypores are, e.g., *Gloeophyllum carbonarium* (Berk. & M. A. Curtis) Ryvarden and *Antrodia primaeva* Renvall & Niemelä. Furthermore, Penttilä and Kotiranta (1996) have shown that many other wood-inhabiting species strongly benefit of occasional forest fires; the remarkable results of their studies will be published later. Wildfires kill most of the trees of the affected area, but almost always some trees (in particular old

pine) survive even repeated fires (Kolström & Kellomäki 1993). During decades after the burn, the amount of coarse woody debris reaches its maximum in the forest (Karjalainen & Kuuluvainen 2001).

In addition to the characteristics and processes described above, old virgin forests (for instance, Białowieża) have special kinds of substrates, that are almost totally absent from managed forests. The kelo trees make up a good example.

MATERIALS AND METHODS

For the most part this is a review article, based on selected literature and field observations by the authors TN and HK. Data dealing with the age and dating of the kelo trees in northern Finland is based on field studies by the author TW. Here some results concerning the kelo are introduced. The rest of the data will be published and discussed by TW in a later, more comprehensive paper.

In summer 2001 TW collected samples from 376 *Pinus sylvestris* trees: standing dead trees, fallen trunks, stumps, and, in addition, old living trees. The study was carried out in *Pinus* dominated woodlands of Inarin Lappi province, eastern Inari commune, northernmost part of Finland. Samples were collected from two landscapes *ca* 20 km apart. Within each landscape, sample plots were established in a grid of 1×1 km. Each plot was circular, with a radius of 20 m. If suitable wood samples were missing within the plots, additional ones were subjectively established in suitable places near by. The number of grid plots was 83 (altogether in the two landscapes), and additional plots totalled 99. Ideally, samples were taken by selecting at least one representative living pine tree (instead of random samples), one oldest-looking standing trunk, and one old fallen trunk from each study plot. In spite of this partly subjective sampling, the material certainly reflects the life span of dominant *Pinus* in the area, from a seedling to the death and decay of the tree.

Sections cut from the trees were dated primarily on the basis of pointer year method described by Niklasson *et al.* (1994). However, the oldest samples were dated by measuring the thicknesses of the annual rings, and identifying the years by computer, using the ring-width chronology of Lindholm *et al.* (1999) as a reference. The main purpose of the work was to study the regeneration of *Pinus* and the fire history of pine forests.

OLD PINE IN LAPLAND

In the study of the author TW, the pith of the oldest living *Pinus sylvestris* L. tree dated back to year 1407, and, considering the first years from ground to the sampling height, the tree was approximately 600 years old. Living trees 400–500 years of age were common in the material. If estimated from ring-widths, old trees had usually lost their growth vigour gradually, dying during an unfavourable climatic episode. The slow death of standing trees, linked with an accumulation of resin in wood, its drying, and the high proportion of heartwood (in relation to sapwood) seem to be the factors that explain the long persistence of wood without decay. Stumps of vigorous *Pinus* trees, cut during forestry practices in the 1980s and 1990s were often much more strongly rotten than the several hundred years old kelo trunks.

The oldest standing, dead, decorticated tree, whose surface could still be found for dating, had died in the year 1539 (Table 1). The surface (revealing the year of death of the tree) in one fallen log could be dated back to year 1515. On trunks older than this, original surface was no more extant, but if calculated from dating of remaining heartwood, some of them had stayed standing for over 700 years after their death. Some natural stumps <2 metres tall had persisted decay and erosion better still, the latest year (surface ring) of the oldest of them dating back to AD 1167, i.e., the tree evidently died in the end of the 1100s. The life of the most ancient *Pinus* found as fallen log ended approximately at the same time, after AD 1153 (Table 1).

Few studies have been made on dating dead trees in a forest. The only one we found for comparison is a paper of Rouvinen *et al.* (2002); in that

Table 1. Recorded life spans of some *Pinus* trees. Samples taken from those trees in which sapwood surface could be found are listed separately from those in which no surface remained. In the first case the latest year is the death-year of the tree, but in the other case it is the last year recorded in the sample, and the tree died no more than a few decades after this. Due to the extremely slow growth and distorted year rings there may be an error of a few years in some samples. Years in brackets: the earliest recognizable year of those samples in which the pith (and first year rings) had worn off.

Sapwood	Data	Standing kelo		Stump*		Fallen kelo	
Surface		Not charred	Charred	Not charred	Charred	Not charred	Charred
Present	Year ring range of the most ancient sample (AD)	1405–1699	1396–1539	(1692)–1779	1404–1633	1360–1549	1194–1515
	Average time since the death of sample trees (number of years)	128	240	104	239	177	394
	Year ring range of the most recent sample (AD)	1777–1985	1537–1979	1651–1988	1473–1890	1590–1997	(1524)–1805
	Number of samples	43	9	6	4	35	5
Absent	Year ring range of the most ancient sample (AD)	1415–1645	(941)–1235	858–1167**	848–1206	(1267)–1499	(909)–1153
	Average time since the latest year rings recorded from samples (no. of years)	206	362	323	499	256	411
	Year ring range of the most recent sample (AD)	1532–1884	(1451)–1838	(1638)–1888	1473–1780	1777–1933	(1731)–1881
	Number of samples	12	12	10	6	28	31
	Total number of samples	56	21	16	10	63	36

* Stump = standing dead tree height < 2 m

** Deduced from the fire history of the site this sample was charred but charcoal has eroded away during centuries after the fire.

study the most ancient standing tree with surface still intact had died AD 1741, and downed log, respectively, AD 1744. In their systematically gathered material of 66 standing and 16 fallen dead pines (diameter at breast height >10 cm) the average time since the death of the trees was 81 (standing) and 118 (fallen) years. Supposing that majority of their samples were not charred, the comparative numbers of our study are 128 (standing) and 177 (fallen) years (Table 1). Older age of our samples is probably due to two reasons. Firstly, in our study area in Northern Boreal zone, growth season is cooler and shorter than in Middle Boreal zone studied by Rouvinen *et al.* (2002), where decay proceeds faster. Secondly, our samples were selected subjectively and the mean counted from them can not be viewed as true average of all dead trees (Table 1). However, in many cases even the most recently died trees had died long time ago. Charred trees, in particular, were almost always extremely old. The results indicate that the turn over rate of CWD and kelo trees is very slow. Therefore, if kelos are removed from a forest the recovery of this resource in forest structure will take decades or even centuries.

FROM LIVING PINE TO ERODED KELO

The oldest living *Pinus sylvestris* found in Fennoscandia (Norway, Sweden, Finland and adjacent NW Russia) was *ca* 810 years of age (Siren 1961). In natural conditions old pine trees gradually lose their vigour and eventually die while still standing. Usually this will happen when the trees reach 300–500 years of age. On exposed slopes, heath forests and sandy soils such individuals may stay standing for hundreds of years, losing their bark and becoming silver-coloured. In Finnish language such trees are called the *kelo*, and this term is proposed here for common use (Fig. 1). The term has already been used in English texts by Kalliola (1966), Renvall *et al.* (1995) and Niemelä & Dai (1999).

Soon after the death of a pine tree, what was sapwood will be colonized by blue-stain fungi, giving a silvery, grey tone on the debarked surface

Fig. 1. A kelo tree, died rather recently (a few decades ago), as seen from the small branchlets still attached. Finland, Koillismaa prov., Korouoma Nature Reserve, August 2001.

(Fig. 2). Such blue-stain fungi utilize the cell contents, not causing true decay, i.e., decomposition of lignin, cellulose or hemicelluloses. Anyhow, it seems that the penetration of fungal mycelia makes the wood unattractive to most decay-causing fungi. In slowly dying pine most of the wood is heartwood, however, and highly resistant to decay because of terpenes and other antifungal components of resin.

An old standing kelo tree can be identified from younger ones: in trees which have died long ago, only the thickest branches remain, or the whole crown has fallen down from a standing trunk. In old kelo trees sapwood has decayed and worn off in rain, wind and frost (Figs 3–4). What remains is just eroded heartwood, from which bases of branches emerge. Old kelos have usually undergone at least one forest fire during their high age, resulting in partly charred surface. Decay proceeds very slowly in the resin-rich heartwood, and accumulated resin makes wood yellowish in

Fig. 2. Kelo offers excellent timber for building; its grey colour comes from blue-stain fungi. The oldest part of the Luosto Reserve headquarters was built in 1971 when kelo was common in the area in many kinds of forests. Finland, Sompion Lappi prov., Sodankylä, August 1998.

Fig. 3. Section of a 330-year-old, living pine tree, first and last year indicated. Reddish heartwood differs markedly from pale sapwood; a small pocket of decay (white-rot) is seen close to the pith, but otherwise the tree was sound. Finland, Inarin Lappi prov., Inari, August 2001.
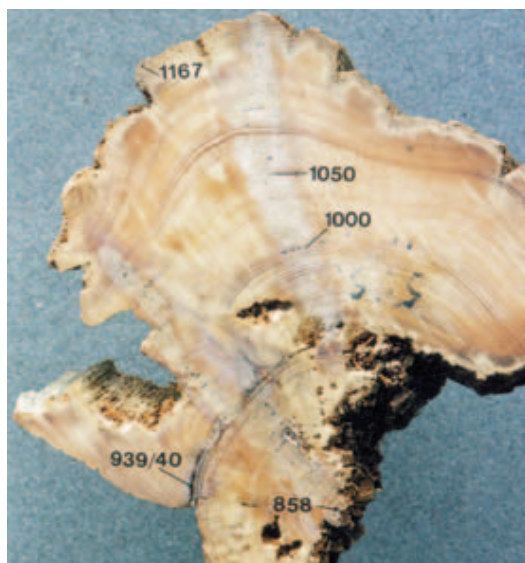

Fig. 4. Section from an old kelo stump, collected from dry *Pinus* dominated forest. Sapwood has decayed and eroded away. Some years are indicated; 939/40 = time of a forest fire, with scar. The tree lived >300 years, and died ~800 years ago. Finland, Inarin Lappi prov., Inari, July 2001.

colour and heavy. Obviously the resistance against decay is a result of the way the tree died, but also of the characteristics of tree individuals, the amount of resin and its chemical composition. Even the scent of a decay-resistant piece of wood differs from such that will decay faster, smelling like tar or turpentine.

Standing kelo trees usually harbour very few fungi. In Finnish Lapland it is usually *Coniophora olivacea* (Pers.: Fr.) P. Karst. that causes the fall of the kelo trees; by its brown-rot the fungus erodes the very base of the tree. After their fall-down the trees become a highly specific substrate for a number of fungal species.

If an old pine tree falls down while still alive, fungal succession, fungal species diversity and the rate of decomposition are essentially different from those of the kelo trees. This is evident, for instance, when studying trees that have fallen down in storms. Then tree trunks are colonized by *Trichaptum* species, *Stereum sanguinolentum* (Alb. & Schwein.: Fr.) Fr. and other rapid pioneers, and after them come *Fomitopsis pinicola* and many other species unfamiliar on the kelo trunks.

THE KELO FUNGI

On Table 2 we list some polypores and corticiaceous fungi that are confined to the kelo trees. The list was made according to the situation in boreal forests of Europe, i.e., the Nordic countries and the Russian taiga. The ecology of some species changes according to the area of distribution, the availability of different host tree species, etc., and therefore such lists would need emendations when applied, for instance, to the situation in Central Europe.

Some species strongly favour the kelo, but can also grow on other kinds of substrates. *Antrodia sinuosa* (Fr.) P. Karst. and *A. xantha* (Fr.: Fr.) Ryvarden are good examples. Many species, however, are strongly linked with kelo trees, and their occurrence in other substrates is quite exceptional. Those examples are indicated by an asterisk in Table 2.

Almost all typical fungi of the kelo have annual basidiocarps. This may be an adaptation to the

moisture conditions of the substrate: the smooth surface of fallen trunk makes it difficult for epiphytes to become established, and hence fallen trunks are subject to desiccation during spells of drought. Some species are sensitive to the amount of rainfall during the season: basidiocarps of *Postia lateritia* Renvall (Fig. 5) are difficult to find in dry years, but they abound in old-growth *Pinus* woodlands if the rainfall was higher than average (Renvall 1992). Some decayers of fallen kelo trees seem to avoid the drought problem by growing their basidiocarps on the underside of a fallen trunk, in a place where the trunk almost (but not quite) touches the ground. For instance *Antrodia infirma* Renvall & Niemelä is usually found just there, in a hidden place where the microclimate is more humid. Likewise, *Antrodia crassa* (Fig. 6), one of the few species with perennial basidiocarps, grows in a narrow gap of the underside, close to place where the trunk touches the ground and absorbs some moisture from the soil. Another perennial species, *Gloeophyllum protractum* (Fr.) Imazeki has another strategy: it seems to tolerate periods of drought, as do its more ephemeral relatives *G. sepiarium* (Wulfen: Fr.) P. Karst.*, G. abietinum* (Bull.: Fr.) P. Karst. and *G. trabeum* (Pers.: Fr.) Murrill. By being poikilohydric (drought-tolerant), the basidiocarps can emerge on the upper sides of fallen trunks, which are more favourable for spore dispersal. Also *Dichomitus squalens* (P. Karst.) D. A. Reid has this strategy, even though its fruiting bodies are annual.

KELO AS A SUBSTRATE FOR FUNGI

What is so special in this kind of substrate? Physical and chemical properties of the kelo trees are characteristic in many ways. During the decades before the death of an old pine, its growth is extremely slow and annual rings are narrow, even less than 0.1 mm, resulting in very dense tissue. In northernmost Europe in climatically the most unfavourable years such trees do not form new year rings at all. Especially in those fire-scarred trees that have survived one or several forest fires, the wood becomes rich in resins, which only few

Table 2. Examples of wood-inhabiting Basidiomycetes (polypores and corticiaceous fungi) growing exclusively or strongly favouring fallen *Pinus sylvestris* kelo trees. The most typical species are preceded by asterisk (*). Examples deal with northern Europe; the ecology of some species changes according to the area of distribution.

Species	Notes
POLYPORES	
Anomoporia kamtschatica (Parmasto) Bondartseva	wood in a late stage of decomposition
Antrodia albobrunnea (Romell) Ryvarden	
Antrodia crassa (P. Karst.) Ryvarden	undersides of very thick kelo trees
Antrodia infirma Renvall & Niemelä	undersides of very thick kelo trees
*Antrodia primaev*a Renvall & Niemelä	on charred wood
Antrodia sinuosa (Fr.) P. Karst.	
Antrodia xantha (Fr.: Fr.) Ryvarden	
Dichomitus squalens (P. Karst.) D. A. Reid	on exposed sites
Gloeophyllum carbonarium (Berk. & M. A. Curtis) Ryvarden	on charred wood
Gloeophyllum protractum (Fr.) Imazeki	upper side of logs in sunny sites
Oligoporus sericeomollis (Romell) Bondartseva	preferring charred wood
Postia hibernica (Berk. & Broome) Jülich	early stage of wood decomposition
Postia lateritia Renvall	in dry pine woodlands
Skeletocutis lenis (P. Karst.) Niemelä	wood in a late stage of decomposition
CORTICIACEOUS FUNGI	
Candelabrochaete verruculosa Hjortstam	
Chaetoderma luna (Romell) Parmasto	fallen thick branches of kelo trees
Dacryobolus karstenii (Bres.) Oberw.	favouring still hard wood
Dacryobolus sudans (Fr.) Fr.	favouring still hard wood
Hydnellum gracilipes P. Karst.	strongly decayed crown of kelo
Odonticium romellii (S. Lundell) Parmasto	
Phlebia cornea (Bourd. & Galzin) Parmasto	favouring still hard wood
Phlebia serialis (Fr.) Donk	wood in a late stage of decomposition
Phlebia tristis (Litsch. & S. Lundell) Parmasto	favouring still hard wood
Pseudomerulius aureus (Fr.) Jülich	fallen kelo in spruce-dominated forest
Sistotremastrum suecicum Litsch. *ex* J. Erikss.	
Tubulicrinis spp.	wood in a late stage of decomposition

fungi can stand. Old tree individuals are more voluminous than average – the volume of the substrate has been shown to be a significant prerequisite for the establishment of certain wood-inhabiting fungi (Renvall 1995).

The most typical sites in which kelo trees develop are dry hillsides on sandy, gravely or stony soil. Their natural vegetation is *Pinus* woodland, where the trees grow in spaced stands. Fallen kelo trees are exposed to direct sunshine, devoid of epiphytes almost to the end of their decomposition, and heat and dry up in sunny summer days. Thick branches of the crown keep the trunks uplifted for tens of years, thus letting them dry up; thin-branched spruce, on the contrary, soon gets ground contact along its whole length, staying more

Fig. 5. *Postia lateritia* Renvall, a characteristic polypore of big, fallen kelo trees in dry pine woodlands. Finland, Kittilän Lappi prov., Ylläs – Aakenus Nature Reserve, *Niemelä 7118.*

moist, and decaying fast. Dry pine woodland is a difficult environment for fungi to occupy, and fits to a few species only.

In addition to almost pure *Pinus* woodlands, kelo trees are also found in virgin spruce-dominated heath forests, in which single pines originate for instance from an early stage of forest regeneration after fire. In such forests the scattered, emergent pines can be 300–500 years old even in South Finland, and large indeed. When they develop into kelo and finally fall down, their fungal communities are essentially different from those in dry sites. Such trees are thicker, longer, and they lie in more humid conditions under the shadow of spruce. *Antrodia infirma* and *Pseudomerulius aureus* (Fr.) Jülich, for instance, are found in such places (Figs 7–8).

Different parts of fallen kelos are favoured by different fungi. *Antrodia crassa*, for instance, is found in the thickest part of the trunk, close to its base. The other extreme, *Chaetoderma luna*

Fig. 6. *Antrodia crassa* (P. Karst.) Ryvarden grows on undersides of thick fallen kelo trees, mostly in old dry pine woodlands. Finland, Koillismaa prov., Korouoma Nature Reserve, *Niemelä 7085.*
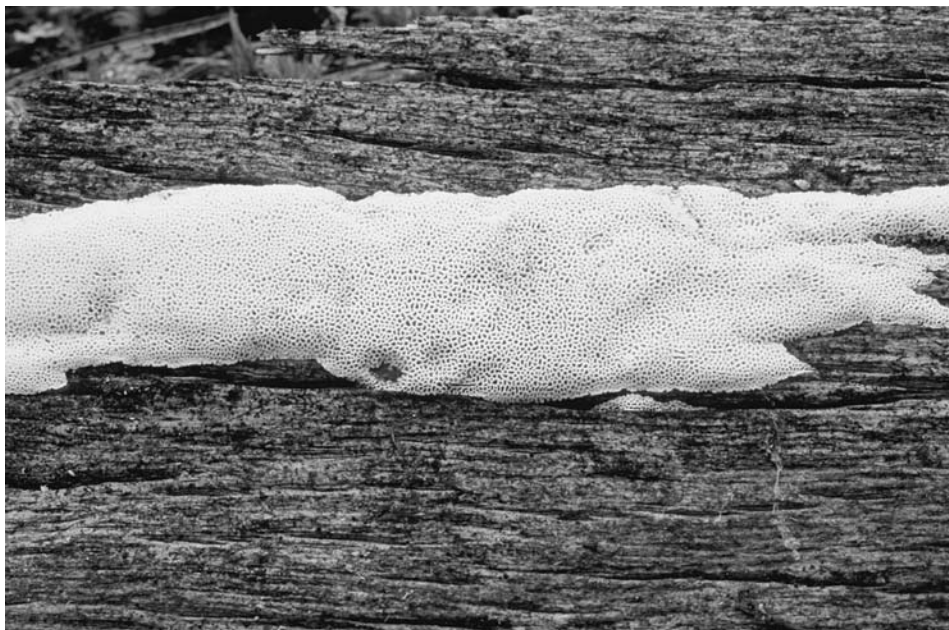
Fig. 7. *Antrodia infirma* Renvall & Niemelä is a rare inhabitant of very thick kelo trees which have lain on the ground for many years, usually in spruce – pine mixed forests. Finland, Koillismaa prov., Korouoma NR, *Niemelä 7024*.

Fig. 8. *Pseudomerulius aureus* (Fr.) Jülich is bright yellow-coloured fungus, mostly growing on fallen kelo trees in spruce – pine mixed forests. Finland, Kittilän Lappi prov., Ylläs – Aakenus NR, *Niemelä 7122*.

Fig. 9. *Chaetoderma luna* (Romell) Parmasto, a corticiaceous fungus which typically grows on thick branches, fallen from kelo trees. Finland, Kittilän Lappi prov., Ylläs – Aakenus NR, 24 Sept. 2001 (no coll.).

(Romell) Parmasto (Fig. 9), inhabits old, eroded, fallen branches. *Antrodia albobrunnea* is more versatile, but mostly occupies the trunk in the crown section of a fallen tree.

Like in all fallen tree trunks, also in the kelo trees fungal composition has its own succession in the course of decay. Some species occupy trunks when they are still hard wood, e.g., *Postia hibernica* (Berk. & Broome) Jülich, while others are adapted to the late stages of decay (see notes in Table 2). Unlike in fallen spruce or freshly fallen pine, the speed of decomposition is extremely slow in the kelo logs, and hence also its fungal succession proceeds slowly. Charred wood, deriving from forest fires, makes a special niche for certain polypores and corticiaceous fungi.

SUMMARY

Kelo is a vanishing nature resource, even though the tree species, *Pinus sylvestris*, is common throughout Europe. The data presented above give an idea of how slowly renewable natural resource we are dealing with. According to Rouvinen *et al.*

(2002) the rate of kelo formation in a *Pinus* dominated landscape may be only one dead tree per hectare in a decade.

Modern forestry practices do not allow pine trees to grow old enough for kelo to develop. Kelo logs make excellent timber for building houses (Fig. 2) and other constructions. In some remote areas of the north it is still used as fuelwood, and paper companies make pulp of it. It takes up to 300–500 years for a dominant pine in a forest to grow old enough to die naturally; it may stand dead for another 200–500 years, and after that lie on the ground for at least several decades, in order to serve as a substrate for the specialized fungi. That would be a most unlikely process today.

Fungi living on kelo trees seem to be very slow in their establishment and growth to a fertile stage. Being highly specialized, their survival on other substrata is unlikely, if the main host is not available. Therefore a break in the supply of the kelo logs in a forest will soon lead into the disappearance of the corresponding fungal species from the area. Most fungi adapted to grow on kelo trees are sparse in number, individuals living far from each other. Therefore only large areas of old-growth forests can sustain viable populations of those species. They certainly make a good example of threatened species.

In southern Finland kelo trees are much rarer than in northern Finland (Kalliola 1966), in practice found in forest reserves only. However, in adjacent Russia kelos are common also in southern parts. The difference is evidently due to longer and more intensive use of forests in southern Finland, than in the north and east. In Russia there was a broad border zone in which forest cuttings were minimal before the 1990s. In Central Europe kelo trees are mostly extremely rare, with at least one exception. The Białowieża forest is one of the very few remnants of the previously extensive Central European lowland forest; kelo trees are commonly seen there. We assume that kelo was a common nature resource throughout Central and South Europe before man started to extensively cut primeval forests *ca* 2000 years ago. Due to the disappearance of this resource, also a great number of specialized fungi vanished from the area. In

fact we cannot even know today, which fungal species and communities were characteristic of the kelo trees in those more southern areas of Europe.

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